THE

NEW PHYTOLOGIST.

A BRITISH BOTANICAL JOURNAL,

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IN CONSULTATION WITH THE STAFF OF THE CAMBRIDGE BOTANY SCHOOL.

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INDEX OF SUBJECTS.

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NOTE.   The titles in small type are those of letters to the Editor on the
Reconstruction of Elementary Botanical Teaching.

CORRIGENDA.

Pp. 64, 65.   The graphs Figs. 5 and 6 should be transposed.
Fig. 5 relates to chloroform and Fig. 6 to mercuric
cyanide, as may be seen from the description in the text.

BOTANICAL WORKS

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Arnold Arboretum, Publications of the. No. 4. Plantæ Wilsonianæ, an enumeration of the woody plants collected in Western China for the Arnold Arboretum of Harvard University during the years 1907, 1908, and 1910, by E. H. Wilson, edited by C. S. Sargent, parts 1—4, 8vo, 1911-14. £2 10s
To be completed in 6 parts.

—— The same. No. 5. **Shaw (G.) The genus Pinus,** 39 plates, 4to, 1914. £2 12s 6d

Bancroft (K.) A handbook of the fungus diseases of West Indian Plants, 6 plates, 8vo, *boards*, 1910. 4s 6d

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Darwin (C. and F.) The power of movement in plants, engravings, 8vo, *cloth*, 1880, 15s

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Jussieu (A. L. de) Genera plantarum secundum ordines naturales disposita, 8vo, *calf*, 1789. 12s 6d

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———— the same, 2nd edition, 8vo, *cloth*, 1909. 10s 6d

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Kew, Royal Gardens, Bulletin of miscellaneous information, 1887-1914, (and) Additional series, parts 1-10, plates and engravings, 38 vols, roy8vo, buckram, 1887—1914. £15

Complete sets of these periodicals are now seldom
if ever obtainable.

THE NATIONAL UNION OF SCIENTIFIC WORKERS.

A T the request of the Executive Committee we enclose in the
present issue of the New Phytologist a memorandum on
the aims and provisional constitution of the organisation which has
recently been formed under the above title. This act is not to be
taken by our readers as equivalent to an editorial expression of
approval of the Committee's statement, but is rather an expression
of the belief that any proposal for the establishment of a national
organisation of men and women of science has a *primâ facie* claim
on the very serious attention of all scientific workers, and certainly
not least of botanists.

We do not propose to discuss the memorandum in detail at this
time, but we should like to suggest the view that the Committee
may actually be taking that " false step " which " might be disas·
trous " " by exciting antagonisms " among those scientific workers—
probably, we think, numerous and many influential—who are
exceedingly unlikely to approve of the formation of a Union, *the
aims* (not *one* of the aims) of which are specifically stated to be
" the promotion by corporate action of the economic interests of its
members." It is true that the Committee are at some pains to
explain and qualify this statement of aims, but the explanation and
qualification do not remove the objection referred to, so long as
this resolution stands alone as the key resolution of those who are
promoting the formation of the Union, and especially since it is
emphasized by the remark that " economic questions must always
be the primary concern of the association."

We must not be misunderstood. We are not prepared to deny
that the formation of an association having the functions of a trade
union may be necessary, in order to give the individual scientific
worker a status commensurate with the importance we all hope
his work will acquire in the future national life ; and if any union
of the kind is to be formed it is clear that it should be on a strictly

representative and democratic basis.   But here we have a union whose "primary concern" is economic, with a suggested 'hinter-land' of other objects, as yet undetermined.   It may be insisted that the memorandum is provisional and that the aims may be entirely revised at the first general meeting.   Nevertheless, no one can avoid judging of the desirability or otherwise of a proposed organisation by the declared aims of its promoters.   And taking the memorandum as it stands it is difficult to avoid the judgment that the union proposed would have its place rather in the world of Labour than in the world of Science.   The interests of science and of scientific work would seem to deserve at least an equal place with the economic interests of its members in the programme of a union of scientific workers which aspires to be more than a mere trade union.

It might perhaps be possible to form a professional association of scientific workers, having something in common with the British Medical Association, the Law Society, the Institute of Chartered Accountants, and similar bodies, though it would of course have no statutory powers and its organisation and functions would necessarily differ from those of any of these bodies in many important respects The primary difficulty is of course the want of cohesion among scientific workers and the very wide range of their interests and activities.   But we see no insuperable difficulty in combining the economic objects of a trade union with the promotion of the interests of science and scientific work, in definite and carefully considered ways, and we suggest to the promoters of the Union that they should consider the point with attention.   Unless something of the kind is attempted it seems unlikely that the proposed union will meet with the practically universal support which is essential if it is to attain its economic objects.

THE RECONSTRUCTION OF ELEMENTARY BOTANICAL TEACHING

THE EXAMINATION OF A WITNESS.

" And he looked for judgment, but behold oppression."

The Five[1] *Wise Men.* (The Authors of the recently published edict.[2]) It has been brought to our notice that in a syllabus of elementary lectures on Botany for which you are responsible you have the effrontery to quote Darwin's statement that Morphology may almost be said to be the " very soul " of Natural History." How do you justify a quotation at once misleading and dangerous unless it be that you are primarily concerned with the history of the dark ages of the science ?

Witness. At an early stage of his botanical career a student should be introduced to different samples of the plant kingdom. The mere description of the parts of which plants are composed is necessarily dull and without any obvious bearing on general problems. If, however, it is possible to awaken his interest—an aim of fundamental importance—by comparative treatment of the types passed under review, and by explaining the meaning and evolutionary significance of homologous organs, the subject of morphology serves a useful purpose. Whether we reject or accept Darwin's conclusions, it is at least worth while to illustrate by comparative treatment of plant organs the nature and meaning of morphology. Regarded merely as an academic exercise, the discussion of morphological problems in relation to evolution stimulates the student's reasoning powers and imagination, an end in itself not wholly contemptible.

T. F. W. M. That is all very well, but is this sort of thing likely to lead a student to regard plants as living organisms ? Is not the study of morphology sterile and deadening ?

W. The aim of a teacher should be to present plants as living machines performing work, to keep constantly in mind both structural features and physiological activities, and—beginning with the lower plants—to illustrate the gradual elaboration of more and more complex mechanisms, also a corresponding increase in the division of labour among the several parts and tissues. I venture to think

[1] Seven would have been more consistent with tradition.
[2] NEW PHYTOLOGIST, Vol. XVI, p. 241.

that no intelligent person can form a true conception of the working of a machine until he knows something of its parts and of the processes by which complexity has been evolved from simplicity.

T. F. W. M. Do you then admit that physioloy is worthy of a prominent place in an elementary course?

W. Yes, the idea that practically all elementary teaching is so far dominated by morphology that physiology is disregarded is new to me. It is true that some botanists have devoted their leisure almost exclusively to morphological problems. "No man," it has been said, "can be a pure specialist without being in the strict sense an idiot": taste or inclination determines what particular kind of idiocy one adopts. But I am now concerned with elementary teaching, and my conviction is that it should be based on a dual treatment of plants, morphological and physiological.

T. F. W. M. But why not, if we may descend for a moment to the jargon of the day, "wash out" most of the morphology and confine yourself to such structural details as are necessary to illustrate the principle of division of labour and the general adaptation of plants to land-life?

W. The difficulty is to decide upon the minimum amount of morphology that is necessary. I maintain that the student ought to have some knowledge of the more important morphological features as well as an acquaintance with the reproductive phenomena of plants selected from each group. To attempt to provide students, whose future work will lead them along various and diverse paths, with a mere smattering of morphology without giving them at least an insight into the vegetative and reproductive phenomena of each group would be educationally unsound. If a lecturer is constantly asking himself whether this or that fact is likely to have a practical bearing upon a student's future work and fears to burden the minds of his pupils with any theoretical questions connected with phylogeny, if I may venture to use the word, lest such questions should savour of academicism, he is not likely to produce botanists who can adapt themselves to the particular conditions under which they may eventually be placed. There is sound sense in Galton's advice to travellers: "Interest yourself chiefly in the progress of your journey, and do not look forward to its end with eagerness." A training in which morphology plays a reasonable part has a high educational value, and experience has shown that such training provides a solid foundation for the various applied sciences in which botany plays a prominent part. It is true that some of the simpler

aspects of genetics, for example, can be presented in an interesting form to a beginner who knows little or no botany, but the aim of the teacher should be to plan his elementary course so that students may be in a position both to appreciate the difficulties that will inevitably confront them and to use their knowledge of morphology and reproductive processes as a starting-point for further enquiry. The student must be in a position not only to state what is meant by genetics but to tackle the subject with intelligence.

T. F. W. M. Is it not a mistake to burden students with anatomical facts which inspire no enthusiasm?

W. The study of anatomy is not uninspiring particularly if treated, as far as possible, from a physiological point of view. It is easy for a man to make out for himself the structure of a plant organ; he has the satisfaction of a discoverer who sees as the result of his own handiwork the complex mechanism of which the plant consists.

T. F. W. M. We are informed that you have given some attention to the study of fossil plants; is this correct?

W. Yes.

T. F. W. M. Has it ever occurred to you that the predilection for this subject on the part of not a few botanists in this country, including, we regret to add, some of the younger generation, has had a pernicious effect on British Botany? Is it fitting that a teacher who deliberately chooses to spend the greater part of his leisure in endeavouring to interpret " aged-dimmed tablets traced in doubtful writ " should be entrusted with the training of men and women who wish to become botanists, gardeners, or planters of waste lands? Is not your soul destroyed " and every part about you blasted with antiquity? " Do you suppose that even the most intimate knowledge of the anatomy of a *Lepidodendron* would be of the very slightest value to anyone confronted with the problem, shall we say, of cultivating potatoes?

W. This aspect of palæobotany is one which I have not hitherto considered. I remember hearing a rumour many years ago that Professor Williamson had a *Lepidodendron* growing in his garden at Fallowfield, but if it was there it was very jealously guarded and I never met anyone who had actually seen the plant, nor do I know whether the method of cultivation employed was similar to that most suitable for potatoes.

T. F. W. M. Have you ever heard of Ecology?

W. My knowledge is extremely limited; "I never even lectured upon it," or to be accurate, I never gave a course of lectures on Ecology. I have, however, gleaned one fact from a perusal of ecological iterature; as Huxley said of holastic philosophy, "it is surrounded by a dense thicket cf thorny logomachies, and obscured by the dust-clouds of a barbarous and perplexing terminology." Ecology has this in common with palæobotany ; it has attracted several botanists who formerly devoted themselves to other fields of activity. It may be that ecologists, unlike palæobotanists, have chosen the narrow path. Most teachers, I suppose, endeavour to explain to their students the nature of the problems with which the ecologist is concerned, and encourage them to study the social life of plants in different habitats. On the other hand it would seem that the solution of ecological problems is a task demanding a thorough training in general botany, to say nothing of ancillary subjects. Ecology, a subject concerned with the relation of plants to their habitats, aims at solving some of the most fundamental questions in biology and requires, more than most branches of botany, on the part of those who study it in the right spirit a very wide and intimate acquaintance with plant physiology and anatomy. It is not, in my opinion, a subject which can profitably be included, except in the most general way, in an elementary course. A statement of the aims of the ecologist is desirable and stimulating, and opportunities should be seized of illustrating the bearing of facts or phenomena met with in the laboratory on ecological problems, but a course of elementary instruction in which ecology bulks largely must, I venture to think, be deficient in the essentials of a firm botanical foundation.

T. F. W. M. Is it then your view that existing methods are satisfactory and that you fail to appreciate the gravity of the present state of things even after our solemn warning ?

W. No teacher worthy of consideration is thoroughly satisfied with his methods. The proposals which you, Sirs, have made are many of them sound, if I may say so without impertinence, but there are practical difficulties only too familiar to many botanists who have had prolonged experience of elementary teaching. May one hope that on a future occasion you will see fit to give weaker brethren some advice, based on your own experience, how best to meet some of the difficulties ? One of the difficulties is limited time, and another is the large size of some elementary classes. The question is, what subjects are most important to a beginner, and

how can they best be presented in a form which is at once interesting and educational ? The range suggested in the recent encyclical is too vast for the time at the disposal of elementary students : an attempt to accomplish all that is demanded would, I believe, end in failure. At the end of the course the students might feel competent to practise many useful arts based on botanical knowledge, but their acquaintance with the fundamentals of pure botanical science would, if one may suggest the possibility, be very much less satisfactory than under present conditions. My contention is that while it is most helpful to discuss possible means of improving our schemes of teaching, and most important that we should endeavour to mend our ways, our reconstruction programme is too destructive and advocates short cuts to the useful at the expense of thoroughness. If a lecturer succeeds in awakening the interest of his students and assists them in their efforts to penetrate into the mysteries of plant-life he achieves something, but if he overburdens his lectures by attempting to meet the manifold future needs of his pupils he is doomed to failure. It is not the extent of information that is important but the quickening of the spirit of inquiry and the provision of a solid basis.

T. F. W. M. Are you content with the present scale of payment to botanists ?

W. No, I cordially agree with your remarks on the pressing need of reform in this matter. I am also strongly in favour of the institution by Universities of pension funds which are urgently needed on general grounds and, one may add, the adoption of a pension scheme, carrying with it compulsory retirement, would no doubt accelerate the realisation of the new demands by facilitating the disappearance of teachers who have lost much of their plasticity and of their power of adapting themselves to revolutionary tendencies.

T. F. W. M. You may have noticed that we call for a new spirit and new ideal.

W. Yes, this demand is a familiar one ; it recalls the exhortations of preachers of other doctrines than those of natural science. As regards the more concrete proposals, I would suggest that the publication of an outline syllabus of an ideal course of lectures and practical work might serve a useful purpose. Teachers who wish to mend their ways would then see more clearly on what lines to proceed, and by a perusal of a syllabus which has stood the test of

experience they would be able to approach the task imposed upon them with greater confidence.

One more word: I would submit that it is undesirable that the study of Botany should be organised on the rigid lines of " Infantry Training." Teachers are not all alike either in their tastes or aptitudes. A teacher should have the courage of his convictions and sense enough to profit by experience, but unless he follows the lines which he feels give the greatest scope to such powers as he possesses his teaching will become half-hearted and dull.

T. F. W. M. No useful purpose is likely to be served by prolonging this examination: you may stand down.

SOME PRACTICAL SUGGESTIONS.

SIR,

For some years past I, evidently in common with other botanists, have felt uneasy regarding the condition of botany in this country. During the past three years, circumstances have permitted me to view botanical activity from the outside, and I had come to the conclusion that unless a drastic reformation took place, botany as a science of living beings was doomed: instead of being a branch of biology it would become a branch of necrology. The memorandum on the Reconstruction of Elementary Botany Teaching has given me much pleasure since it has raised the hope that botanists will combine to force an improvement: individual efforts, and of these many have been made, are all but valueless.

The reason for the present state of affairs is primarily due to the preponderance of morphology, which has adversely affected not only the training of students but also original investigations and researches; indeed, an onlooker might well be excused if he concluded that modern botany in some of its aspects approached the scholasticism of the middle ages.

The memorandum raises points for discussion too many to consider in the present communication. I should like, however, to remark on the following :

1. *SCOPE.*—I am in substantial agreement with the concrete proposals set forth in the memorandum. It is essential that a student should not be allowed to take an Honours degree in any subject without first taking the Pass. A candidate for the Pass must, of course, take a certain number of subjects, and it is important that a candidate for Honours in Botany should not be allowed an unlimited choice of subjects for the Pass degree. Assuming that in addition to botany two other subjects are necessary, I would suggest that some such grouping as follows should obtain :—

(1) Chemistry or Geology.

(2) Physics or Geography, provided Geology is not taken as an alternative to Chemistry.

(3) Mathematics.

The main idea is to prevent a student taking a combination of similar subjects. For this reason Zoology does not find a place, since, from the educational standpoint, it does not appear desirable to have a second subject which is almost entirely morphological.

With regard to the Pass Course, a reasonable familiarity with the British Flora is desirable, and all students should be able to use a Flora. Similarly, all candidates for Honours should have some knowledge of economic botany; there should be no difficulty in introducing the subject in all of the three types of school suggested.

2. *STAFF.*—It is generally true that most departments are understaffed. The head and his subordinate heads (if there happens to be any) are responsible not only for teaching but also for organisation and administration, in addition to which much outside work has to be done. Their spare time may be devoted to original work. Practical classes almost invariably suffer from too few demonstrators. This is particularly true of practical classes in plant physiology in which there should be one demonstrator for each eight or ten students if proper training in this branch of the subject is to be given. Further, there are very few botanists—I can only think of one, and he would disclaim it—who are sufficiently conversant with the advances in knowledge of chemistry and physics to conduct classes in advanced physiology entirely by themselves. The staff of each botany department should, therefore, include a chemist and a physicist. This is essential if one of the honours school is to be biochemistry and biophysics.

3. *TEACHING.*—Signs are not wanting that the quality of teaching of botany has fallen off in recent years, a fact probably due to an overloaded syllabus with the inevitable examination looming in the distance. The resulting tendency is that both teacher and student try to accomplish too much. Further, there is too much lecturing and too little teaching. This deterioration in teaching appears to be true not only with respect to theoretical but also to laboratory work. The practical training in vegetable physiology leaves much to be desired; too much standard apparatus, bought ready made, is used, with the result that it is very rare indeed to find a student who can, at the end of his course, design an apparatus to demonstrate a particular phenomenon with which he is generally familiar, but which he did not happen to do in his course in the particular form presented. Progress cannot be made unless each problem, no matter how simple it may appear, is clearly presented to the student's mind. The reason for each piece of apparatus must be clearly understood, and the causes of failure and of peculiar and unexpected results must be ascertained. Every student should make up his own apparatus as far as is possible.

Finally much better results would be obtained if the study of function went hand in hand with morphology; it is an anomaly that physiology should be relegated to a special course, at the end, say, of the summer session; when such is the case, it is hardly surprising if the student concludes that vegetable physiology is a curious kind of special subject having some connection with plants but not much with botany.

A point for discussion is the advisability of continuous courses, *e.g.*, chemistry during the first term, geology during the second and botany during the third term, as opposed to concurrent courses. I have seen both in operation, and am unreservedly in favour of one term, one subject.

Finally, in view of the fact that the classes in some botanical centres consist almost entirely of medical students, the teaching of botany to medical students would appear to be within the scope of the memorandum. The subject has its peculiar difficulties, so that it would, perhaps, be better to raise the question in a separate communication.

4. *EXAMINATIONS.*—Students naturally desire to pass the various tests laid down, and this by the line of least resistance. The majority of the examinations do not test the candidate's *education* or capabilities, they merely ascertain the capacity of his memory, This the student knows and also the teacher, and, unfortunately there are still some teachers who consider that the examination is the goal.

There is a further aspect: I remember some years ago a friend wrote to me that he was up for his final next month, and would I kindly give him a few tips. I told him that if he would let me know who the examiners were I would think it over. This I did, on receiving the names of the eminent botanists, and sent a list of likely subjects: Nine appeared in the papers! My friend did remarkably well, and on meeting him during the vacation, I noticed that when I congratulated him on his success he appeared somewhat constrained in manner; some time afterwards he remarked. " I say, it was awfully good of you to send me those tips, but as a matter of fact I didn't look one of them up," on hearing which my conscience was much relieved.

Most agree that examinations are necessary, so that, in order to obviate their undesirable features, they must be conducted on lines which will really test the candidate's education and capa

bilities. Much improvement would result if all examining authorities ceased to publish a detailed syllabus, and contented themselves with a general statement regarding their requirements. In the examination itself, much more stress should be given to the practical papers which should be conducted under conditions as unconstrained as possible, the candidate being given ample time. A properly conducted practical test is the best means of ascertaining the candidate's capabilities.

A candidate should be given credit for work done during the course. The marks allotted should be in proportion to the maximum obtainable at the examination, and should be based on a carefully thought out scheme in order to avoid the obvious pitfalls.

5. *RESEARCH.*—The memorandum states " Research or at least, a practical introduction to the methods of research should be an integral part of graduation work in the honours school. . . ." It is doubtful if any will disagree with this suggestion provided that it does not mean that publication of results is of a necessity to follow. Personally I feel that Editors are too kind hearted and sometimes publish papers in order to encourage young botanists. By so doing, the standard is lowered. Most working botanists over a certain age must have remarked that some papers contain nothing new, and are built up of facts which are familiar to anyone with a more or less extended laboratory experience.

6. *CONCLUSION.*—When a sufficient number of botanists have expressed their opinion on the present question, I should like to suggest that the Editor convene a small central committee of representative and responsible botanists to consider the whole question and to agree on a course of action. The result should be communicated to the teachers of each University, or corresponding institution, who should devise the plan of action suitable for the local conditions. It is desirable for the central committee to be permanent in order that advice may be given to ocal committees, and action co-ordinated.

I am, Sir,
Your obedient Servant,
T. G. HILL.

THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.

By James Small, M.Sc. (Lond.), Ph.C.

Chapter IV.

THE COROLLA.

THE main characters of the corolla may be divided into four groups—form, development, colour and vascular anatomy, and, in addition to the presentation of the facts concerning these characters, the present chapter includes the history of our knowledge of the corolla in the Compositæ and a discussion of the bearing of the facts and the theories of variation in the corolla upon our general problem of the origin and development of the family.

A. History of the Corolla in the Compositæ.

The history of the corolla begins with the observation by Theophrastus (see Chap. I, Section A) of its epigynous position. During the period of the herbals very little attention was paid to the floral characters. Among the early writers, Lobel (49) seems to have considered the corolla in grouping his genera and Caesalpino (14) used the colour of the corolla to sub-divide his Class XI, the Anthemides, which included practically all the Compositæ not in the Cynareæ or Cichorieæ.

Morison (57) used the colour of the corolla and the presence or absence of rays in his sub-divisions of the Compositæ; Ray (69) and many systematists in the succeeding period followed his example. The discoid, rayed and "semi-flosculose" (Cichoriaceous) condition of the corolla furnish the diagnostic characters for the main divisions of the family in Tournefort's system (81). Boerhaave (8) separated the Cynareæ from the other discoid forms and endeavoured to place these latter among related genera, distinguishing radiate and discoid forms.

After the definite establishment by Vaillantus (86) of the sections, Cynarocephalæ, Corymbiferæ and Cichoraceæ very little advance was made in the use of the characters of the corolla until Cassini published his analysis of the corolla (16); the chief point to be noted is the establishment of the Labiatiflorae (Mutisieæ) by De Candolle and Lagasca. Berkhey, in 1760, (7) considered the corolla in some detail but added nothing new. Gaertner, in 1791 (31), returned to the Radiatæ and Discoideæ of the earlier

systematists. Bentham (see Bib. I, 7) confirmed Brown's statement
(10) of the universality of the valvate aestivation of the corolla in
the family and considered the characters of the corolla as important
for purposes of classification. Robertson (72) mentions a curious
point concerning the receptacular bristles in *Echinacea* spp., which
protect the flowers from bees and adapt them to butterflies by
increasing the functional length of the nectar tube beyond that of
the corolla.

The only observations of the "absciss-mechanism" of the
corolla seem to be those by Yapp (98).

In connection with the popular explanation of the enlargement
of the corolla of the ray florets at the expense of the stamens,
Uexküll-Gyllenband (85) adduces numerous examples of (1) reduction
in the stamens with no reduction in the corolla, (2) enlargement of
the corolla with no reduction in the stamens, (3) reduction in the
stamens with reduction also in the corolla, and (4) reduction in the
stamens with both enlargement and reduction of the corolla in the
same species. It may, therefore, be considered proved that there
is no correlation between the enlargement of the corolla and the
absence of the stamens in the ray florets.

The detailed history of the corolla subsequent to Cassini may
be most conveniently given in various sections as follows :—

Development. The first account of the floral development in the
family is by Buchenau (12, 1854), who extended his observations
in a later contribution (13). Two years later Cruger (22) showed
clearly that the corolla was differentiated before the pappus, and
the following year the study of the subject reached its highest point
in Payer's clear and elaborate exposition (67). Payer confirmed
the late appearance of the " calyx " and the early appearance of the
posterior split in the Cichorieæ. Weber (89) considered that the
corolla in the Cichorieæ and that of the ray florets in other tribes is
an entire tube which is split only by the growth of the style and
stamens when the corolla is quite mature. Kohne (46), Buchenau
(13) and Payer (67) all agree in observing the early posterior split
in the Cichorieæ and the abortion of the posterior lip in the ray
florets. Hildebrand (36) gives the usual account with a few figures,
but Payer's figures are the best yet published. Cramer (21) treats
of the Compositæ, but considered only the ovule in detail.

Our knowledge of the development of the corolla was extended
to the " Labiatifloræ " by Hänlein (35) who considered that the

bilabiate corolla showed a development intermediate between that of the ordinary ray corolla and that of the tubular corolla.

Coulter (20) considered that the primordia of all four sets of floral organs are blended at first and that the late appearance of the calyx is due only to the late development of its upper portion. Martin (51) agrees with Coulter and points out that of necessity the " calyx-tube " must be the first part to appear. As no demarcation can be observed between the ovary wall and the so-called calyx-tube it would seem more in accordance with modern nomenclature to describe the undifferentiated primordium as the receptacle of the flower.

The most recent contributions are those by Merrell on *Silphium* (54) and by the writer on *Senecio, Calendula* and *Taraxacum* (81). Merrell again confirms the corolla as the first floral part to be differentiated and goes into many interesting details of the other parts of the floret.

Colour. Hildebrand in his elaborate treatise (37) includes a number of observations on the Compositæ. He established the colour sequence—green, yellow, white, red, violet, blue—by observing the following facts—blue flowers vary to violet, red and white vary but seldom to yellow; red flowers vary more to yellow than do blue flowers; yellows may vary to blue but more often to red; green flowers give yellow and white flowers; yellow gives orange with red plastids and the colour of the sap gives reds and blues.

Müller's contributions are extensive but he gives two very useful historical accounts (60-61). The views expressed in one of
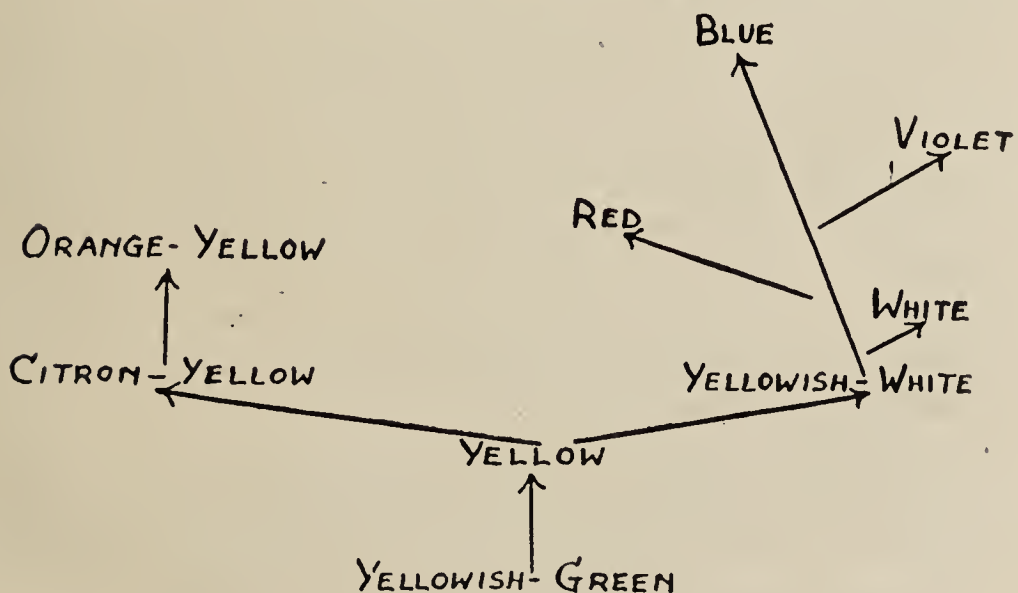
Fig. 8. Evolution of colour according to Müller.

his earlier papers (58) may be given as a diagram, Fig. 8. In his Alpenblumen (59), Table II, p. 481, his figures for the insect visitors to yellow and to white flowers are very similar, but he gives the colour sequence—greenish-yellow, yellow, yellow with orange red spots, white, white with yellow spots, rose red, deep red. From other tables butterflies and even bees seem to prefer yellow to white.

Avebury (2) considers that blue flowers have evolved from green flowers by passing through the intermediate stages of white or yellow and generally red.

Grant Allen (1) gives a similar colour sequence, but in considering the Compositæ he takes the Cynareæ as primitive on account of their highly developed colours and states that reversion in colour has been the rule throughout the family because " the primitive ancestral composite had reached the stage of blue or purple flowers while it was still at a level of development corresponding to that of the scabious or *Jasione.*" He also considered that the " Ligulates were again developed from the yellow-rayed Corymbifers by the conversion of all the disk florets into rays."

Observations by Willis and Burkill (92) confirm the general sequence. Table XII (92a) shows yellow above white but Table XIII (*loc. cit.*) shows a decided preference by the higher insects for white.[1] In most of the tables given white is seen to be preferred to yellow by desirable visitors and in Table XXXVII (92b) the order of efficiency is given as—rose purple, blue, lilac, white, yellow, green.

De Vries (87-88) gives many examples in the Compositæ of the atavistic variations noted by Hildebrand (37) and also progressive variations where white flowered species have suddenly developed blue varieties, such as *Ageratum cœruleum.* A similar progressive mutation, where a white ray appeared in one capitulum of a normally yellow flowered *Dahlia,* is discussed in its biochemical aspect by Kajanus (45). Other sudden variations in colour are recorded in *Cosmos* by Longo (50). An interesting atavism is recorded by Daniel (23), see also Small (77).

Anatomy. Jacquin (43) and other early botanists who figured the corolla in the Compositæ did not usually indicate the venation accurately ; usually a vein is put in the position of the midrib for

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[1] There are several kinds of whites, see Neilson Jones (64a).

each lobe (see Jacquin, plates 589-595). Berkhey (7) is an exception as he shows the veins correctly in his figures.

Brown (10) was the first to observe the venation of the corolla in detail and gives the disposition of the veins (alternating with the corolla lobes and dividing, then uniting to form an arch to each lobe) as a remarkable point common to all Compositæ. On this character he controverted the removal of the Ambrosinæ from the Compositæ as carried out by various authors from Linné downwards (see Table 1, Chap. 1) In a later contribution Brown (9) gives an account of the history of this subject up to his date, 1818.

Don (27) at a later date duly noted the venation of the Cichoriaceous corolla. He also discussed the vascular supply in *Zinnia* (28) and considered that the corolla was absent in that genus, on account of the peculiar veining of the structure ; the ray being "an elongation of the exterior cortical layers of the ovarium."

Hildebrand (36) gives very good details in Plate I, Fig. 6, of the vascular supply of the corolla in *Taraxacum* and also in other types. The only detailed observations of the vascular supply of the corolla are those by Trécul (83, see also 76) and those by the writer (76).

Anomalous Structure. Anomalies in the structure of the flower, especially the corolla, are dealt with in detail by Masters (52) and at greater length by Worsdell (97). It is, therefore, necessary to point out only a few marked or additional facts.

There are a number of records of floral anomalies in *Helenium autumnale*. The most complete account is that by Worsdell (96). Other accounts have been given by Masters (53) and the writer (77). A proliferation similar to that which occurs in *Helenium* is recorded by Békétoff (6) for *Cichorium Intybus*.

The proliferation known as the "hen and chickens" occurs frequently in a number of genera, see Worsdell (97) and Offner (65). Daniel (24) records some interesting grafting experiments where the interaction of the scion and stock extended to the number of capitula developed.

Depauperation occurs frequently. James (44) gives an account of a solitary capitulum instead of numerous capitula in *Rudbeckia hirta*, but genera with branched inflorescences frequently have one or more more species in this condition, a notable example being *Liabum*, § *Paranephelium*, and a more remarkable example outside the family, *Gardenia Thunbergia*, Rubiaceæ (79).

Another form of depauperation is a reduction in the number

of florets in the capitulum. *Madia sativa* usually has about 25 disc florets and 10 ray florets. *Madia dissitiflora* usually has 3-6 disc florets and 5-8 ray florets. Specimens of these two species were grown in pots in 1916 at Newcastle and both showed only two or three disc florets and two to four ray florets. A similar phenomenon is recorded in *Anthemis Cotula* (3), where the disc florets were entirely absent and from 6-20 ray florets, arranged in the " double " fashion, remained. Fasciated capitula are common, see Worsdell (97), Bailey (4), Bruckman (11) and Palibine (66a).

Two very curious anomalies are the common, if not constant, occurrence of loose florets on the root stocks of *Catananche lutea*, which is recorded by Daydon Jackson (42), and the so-called supernumerary petals recorded by De Candolle (15).

Anomalous Bilabiate Florets. One of the earliest indications of this anomaly is the description of the four-toothed corolla of *Erigeron humile* by Graham (34). Eichler figures (30, p. 286) a bilabiate corolla in *Xeranthemum annuum*. Giard (33, Plate I, Fig. 2) figures a few bilabiate neuter ray florets in *Pulicaria dysenterica*. Celakowsky (17, and see Worsdell, 97, Plate 39) figures a similar structure in *Anthemis austriaca*. Uexküll-Gyllenband (85) figures a two-lipped corolla in *Psiadia glutinosa*, *Heterothalamus brunioides*, *Xeranthemum annuum*, *Erigeron alpinus*, *Centaurea Jacea*, (see Fig. 4, Chap. II), also in *Denekia capensis* and *Petasites* spp. Wettstein (91, p. 468) figures the same phenomenon in *Plagiocheilus peduncularis*. Trow (84, p. 274) figures an irregularly bilabiate corolla in *Senecio vulgaris*. Hoffman (38), in addition to several of the above, figures a bilabiate corolla in *Grangea maderaspatana*. Other examples are *Helenium autumnale* (Fig. 9, 9) and *Chrysanthemum Leucanthemum* (see Traverso, 82). The writer has figured bilabiate forms in *Calendula* and *Dimorphotheca* (77, see Fig. 9, 10-11). The reduced corolla of the honey flowers in *Leontopodium alpinum* recorded by Uexküll-Gyllenband (Fig. 4, Chap. II) were first mentioned by Schröter (73). Müller (61a) and Boeuf (7a) record cases of polymorphism with changes in the size of the corollas of the outer florets.

Chrysanthemum Leucanthemum, var. *tubulifera.* Dickson (26) exhibited specimens of this anomaly, where the ray florets are tubular as is frequently the case in *Helenium autumnale*, at the British Association in 1874. Stevens (80) in 1907, and Traverso (82) in 1911 figured various other irregularities, in the rays of this species.
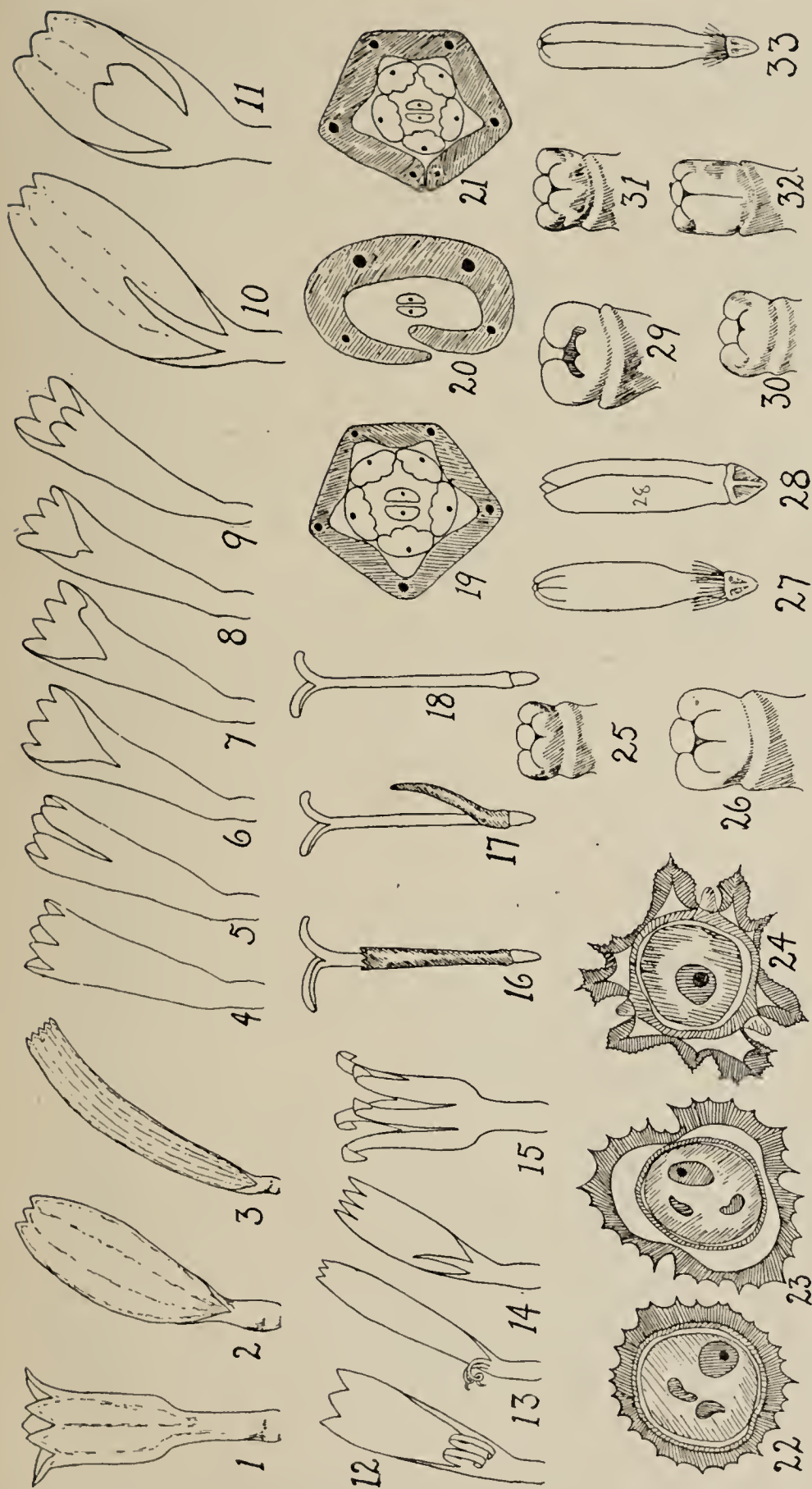
Fig. 9. 1-3, typical corolla forms. 4-9, corolla forms in *Helenium autumnale*. 10, corolla in *Calendula officinalis*. 11, corolla in *Dimorphotheca pluvialis*. 12-15, corolla forms in the Mutisieæ, 12—*Trixis*, 13—*Trichocline*, 14—*Barnadesia*, 15—*Schlechtendahlia*. 16-18, female florets in *Haastia Sinclairi* (after Uexküll-Gyllenband) ; the corolla is shaded. 19-21, tranverse sections of young florets, orientated with axis to left of figure. 19—tubular, 20—bilabiate, 21—ligulate. 22-24, sections of types of pollen grains, 22—Tubulifloræ, 23—Senecio vulgaris (occasional form), 24—Cichorieæ (after Beer). 25-33, floral development. 25-27, tubular florets of *Senecio vulgaris* 28-30, ray florets of *Calendula officinalis*, 31-33, ligulate florets of *Taraxacum officinale*.

Recently the phenomenon was again recorded for Britain by Rea (70) and was named as above in an account by Lindfors (48).

The occurrence of similar tubular ray florets in *Helianthus annuus, Ratibida columnifera*, var. *tubularis, Rudbeckia hirta*, var. *tubuliforme*, and *Gaillardia pulchella*, var. *fistulosa* (*G. fistulosa*, Hort.) is recorded by Cockerell (19), and in *Gaillardia aristata* by Robbins (71).

Mutations. The sudden appearance of these various anomalies adds strength to the evidence for discontinuous variation in the Compositæ. Many examples of such mutations in the corolla and other parts are given by De Vries (87), the origin of *Chrysanthemum segetum plenum* (88) being a particularly clear case of the origin of a variety suddenly under experimental conditions. The origin in nature by mutation of *Arctium minus laciniatum* is discussed by Hus (40).

Ostenfeld (66) has studied the origin of micro-species in *Hieracium* under experimental conditions and gives as his opinion that "very probably, in Europe, new forms of this sub-genus (*Archihieracium*) are appearing at the present time, and it is an interesting fact that many of the described species have an extremely limited distribution, which points to a very recent origin." This last phrase is of great interest in connection with Willis's Law of Age and Area (94 and 74a) which will be discussed later.

Trow (84) has also recorded a mutation in *Senecio vulgaris* and Ishikawa's cytological work (41) seems to indicate the presence in the Compositæ of tetraploid mutations and "pairs of species" as described by Gates (32). Phillipi (68) records another mutation in *Senecio vulgaris*, a gynodiœcious strain.

The anomalous genus, *Fitchia*, was placed in the Cichorieæ by Hooker (39); Nadeaud suggested at first (63) that it should be in the Heliantheæ but afterwards (64) agreed with Hooker. Del Castillo (29) snbsequently placed the genus in the Mutisieæ. Such cases are best regarded as large mutations like those claimed by Willis (93) in the Podostemaceæ, and their study in the light of modern evolutionary ideas, such as suggested by Davenport (25), is sure to be a great help in the attainment of the truly natural classification, which is the aim of the present and future investigations.

Doubling. In addition to the numerous cases of doubling discussed by De Vries (87-88), Molliard describes some interesting

observations on the causes of doubling in various capitulate species (55-56a). In the Compositæ he mentions a doubling of *Matricaria inodora* as due to *Peronospora Radii* (56), and in *Bellis perennis* as due to *Eriophyces* sp. (56a).

More or less closely allied to the phenomenon of doubling is the number of ray florets but as this and the number of involucral bracts and receptacular paleæ seem to be expressions of the relation of phyllotaxis to mechanical laws (see Church, 18, Fig. 46, etc.) the whole matter will be discussed latter in a chapter on phyllotaxis.

B.   Variation in Form of the Corolla.

The main thesis of this section is that the ordinary ray floret of the tribes other than the Cichorieæ has really a bilabiate structure, the inner lip being aborted as a rule but frequently more or less developed. It is, therefore, considered advisable to restrict the use of the term *ligulate* to the five-toothed, properly strap-shaped corolla of the Cichorieæ. The fundamental type, as is well shown by Uexküll-Gyllenband (Fig. 4, Chap. II), is the tubular corolla with a campanulate upper region and five equal lobes. In addition to these three types there is a very narrow, tubular form, Fig. 10, A, which is described as filiform.

The Ligulate Type.

As will be shown later (Section C) the ligulate corolla is easily derived directly from the tubular type by a simple splitting or rather by the failure of the connecting tissue to develop between the two posterior petals. The extreme uniformity of this character in the Cichorieæ confirms the conclusion from the uniformity of the pollen-presentation mechanism that the Cichorieæ are monophyletic. The origin has been suggested to be mutational by the writer (77), who also suggested a recent derivation from the Senecioneæ and gave as confirmatory evidence of the Senecioneal origin the occurrence of a type of pollen grain in *Senecio* (Fig. 9, 23) which is intermediate between the characteristic type of the Tubulifloræ, (Fig. 9, 22), and that of the Cichorieæ as figured by Beer (Fig. 9, 24).

The origin of the Cichorieæ by mutation involves only two marked changes, the development of the ligulate corolla and of laticiferous vessels. The problem presented by the latter change is being investigated and as a first step the latex has been shown to be translocated after the manner of carbohydrates (74). The occurrence of transitions from the ordinary mucilage sacs to laticiferous vessels and the development of laticiferous tissue of

various forms in comparatively distantly related genera favours the assumption that this change can take place with comparative ease.
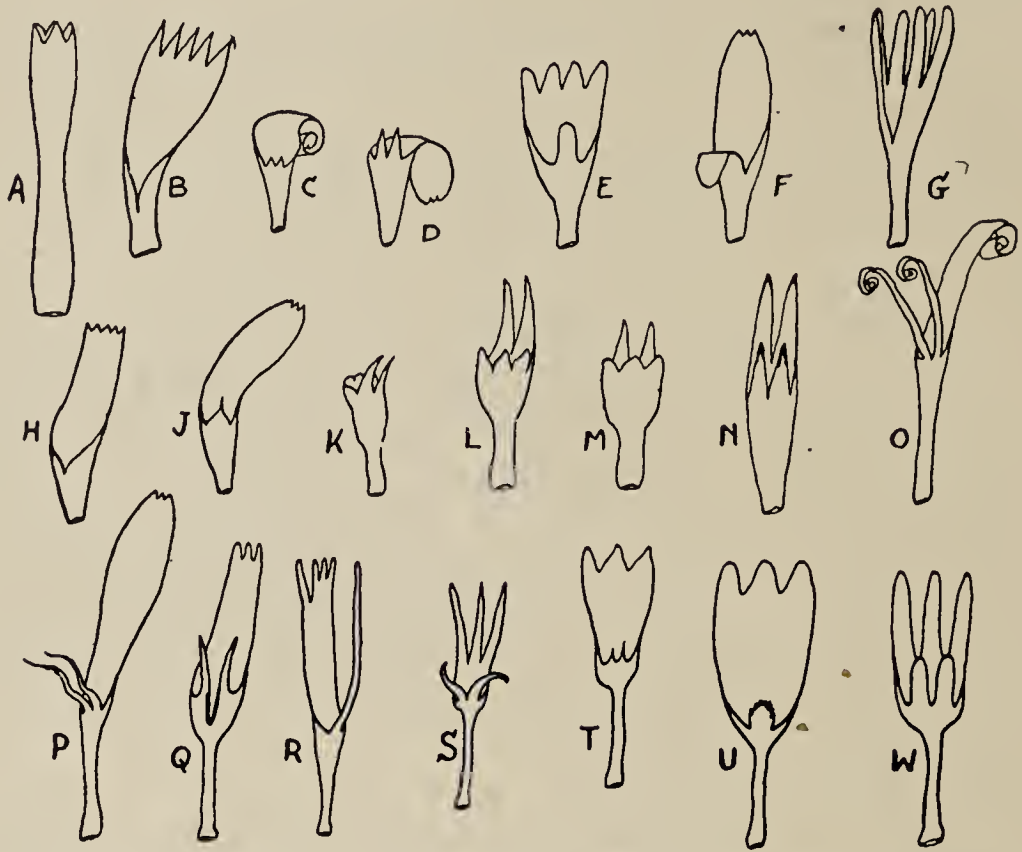
FIG. 10. Corolla forms—A, *Cavea tanguensis*, filiform ; B, *Stokesia cyanea* ; C, *Brachyglottis repanda*, ray; D, *Nassauvia axillare ;* E, *Nanothamnus sericeus*, disc ; F, *Dipterocome pusilla*, ray ; G, *Ainsliæa pteropoda ;* H, *Catamixis baccharoides* (after Thomson) ; J, *Cryptostemma calendulacea*, ray ; K, *Anacyclus clavatus*, disc ; L, *A. clavatus*, var. *inconstans*, disc ; M, *A. tomentosus*, disc ; N, *Siebera pungens ;* O, *Mutisia lanata*, disc ; P, *M. lanata*, ray ; Q, *Erythrocephalum zambesiacum*, ray ; R, *Seris polymorpha*, ray ; S, *Hinterhubera columbica*, *one* variation of ray ; T, *Tridax Mandonia*, ray ; U, *Monolopia major*, ray ; W, *Microspermum debile*, ray.

The origin of the ligulate corolla can scarcely be other than a discontinuous variation, as there is no genus in the Tubulifloræ which shows even rarely the true ligulate corolla. The five-lobed, palmate corolla of *Stokesia* (Fig. 10, B) and the sub-palmate, five-lobed or five-toothed corolla, which occurs rarely in some species of *Elephantopus* (Vernonieæ), *Pentachæte, Lessingia, Pterigeron* (Astereæ), *Chromolepis* (Helantheæ), *Cephalophora, Helenium* (Helenieæ), *Chrysanthemum* (Anthemideæ), *Senecio* (Senecioneæ) and more commonly in several genera of the Cynareæ and Mutisieæ, are ob-ovate and palmately lobed, not oblong with practically parallel margins and five triangular teeth like the corolla of the Cichorieæ.

This palmately lobed corolla is only one particular case of the

very varied development of the bilabiate type. The series given, Fig. 9, 4-9, for *Helenium autumnale* includes one, Fig, 9, 5, which belongs to the palmate type and two others, Fig. 9, 7-8, where the abortion of the fifth lobe is progressing to the complete absence shown in Fig. 9, 6.

The origin of the ligulate type by a mutation seems very similar to the origin of the fimbriate type described by Trow (84). The dropping out of a factor for non-ligulateness in the same way as the supposed factor for non-fimbriateness is suggested to have done, would, with the addition of the presence of laticiferous vessels, give the first of the Cichorieæ.

The Bilabiate Type.

The presence of the posterior lip of the bilabiate corolla occurs markedly in the Mutisieæ, where it is characteristic of four of the sub-tribes and occurs in *Seris* (Fig. 10, R) and *Ainsliaea* (Fig. 10, G) of the Gochnatiinæ, but it is by no means confined to that tribe. In addition to the sporadic appearance of the posterior lip described in *Xeranthemum, Pulicaria, Anthemis, Psiadia, Heterothalamus, Erigeron, Centaurea, Denekia, Petasites, Plagiocheilus, Senecio, Helenium, Chrysanthemum, Calendula, Dimorphotheca* and *Grangea* the phenomenon has been observed by the writer to occur occasionally in the double varieties of *Callistephus, Chrysanthemum, Helianthus,* and *Tagetes.*

One of the posterior petals is frequently developed in the ray florets in most of the tribes giving a 4-dentate or 4-lobed corolla. The usual number of lobes in the anterior lip is three, but these may be fused to give two or the lip may be entire.

In the Senecioneæ a posterior lip is sometimes developed in the filiform florets of *Erechthites* and it is a normal character of the uni-seriate rays in *Brachyglottis*, a monotypic genus very closely allied to *Senecio*, Fig. 10, C.

The posterior lip is also developed frequently in the rays of the monotypic genus, *Dipterocome*, in the Calenduleæ (Fig. 10, F).

In the Arctotideæ *Cryptostemma* shows the character (Fig.10, J).

In the Anthemideæ *Anacyclus*, § *Diorthodon*, D.C. has the ray entire or 3-dentate but the disc florets although sometimes regularly 5-lobed, are frequently bilabiate, the two posterior lobes being narrow and erect while the anterior lip has the normal form (Fig. 10, K-M).

In the Inuleæ *Nanothamnus*, another monotypic genus, has one of the posterior petals of the hermaphrodite florets split off from the

other four down to the base of the limb, thus giving a bilabiate corolla
(Fig. 10, E). Throughout the tribe there are many filiform corollas
with the apex bi-dentate or bi-fid; this is another modification of
the bilabiate corolla.

The outer florets in the Cynareæ show various bilabiate forms,
as in *Centaurea* (see Fig. 4, Chap. II). In *Xeranthemum* (Fig. 4)
and *Siebera* (Fig. 10, N) the corolla of the female florets is constantly
bilabiate with the anterior lip entire or 2-dentate and the posterior
lip dividedin two.

The predominance of the bilabiate corollas in the Mutisieæ
has already been noticed. In *Barnadesia* (Fig. 9, 14) all or only
the exterior florets show a 4 + 1 type of bilabiate corolla. In
the Onoseridinæ the bilabiate corolla as a rule occurs only in
the 1-3-seriate ray florets, but in *Mutisia*, the largest genus,
the condition sometimes extends to the disc florets also (Fig.
10, O-P). The anterior lip has 2-3 lobes or is entire *(Erythro-
cephalum)* and the posterior lip has two lobes (Fig. 10, Q). The
capitulum in the Gochnatiinæ is homogeneous as a rule, but in
Seris and *Ainsliæa* an inequality in the length of the laciniæ of the
corolla makes it sub-bilabiate. The Gerberinæ show great variety
in the structure of the two lips. All the florets in the capitulum are
usually bilabiate, the anterior being entire or 1-4-lobed and the
posterior lip entire, two-lobed or absent. The entire posterior lip
is due to the fusion of the two lobes or more frequently to the
development of one of the posterior petals with the anterior lip to
give a 4 + 1 combination, Fig. 9, 14-15, instead of the usual 3 + 2,
Fig. 9, 12-13. The complete abortion of the posterior lip makes
the ray floret an ordinary one. In the monotypic genus, *Catamixis*,
all five petals are fused and the split is posterior so that something
like a ligulate corolla results (Fig. 10, H), but this is just one more
variation in the manner of splitting and cannot be taken as an
intermediate type leading to the Cichorieæ. In the Nassauviinæ
all the florets in the capitulum are bilabiate, usually with the 3 + 2
combination (Fig. 10, D), but the anterior lip is entire in *Oxyphyllum*
and various other genera show combinations and fusions of the
lobes such as 4 + 1, 3 + 1, 2 + 1, 2 + 2 and 1 + 1.

All these variations prove that the corolla in the Mutisieæ is in
a very mutable condition and, in spite of the explosive irritability
discussed in Chap. III, it is possible that the Mutisieæ is not a
natural group but a collection of bilabiate forms with the addition
of the genera of the Gochnatiinæ, which are scarcely to be

distinguished from the Cynareæ. That a bilabiate corolla is not a character of tribal rank is obvious from the large number of cases where it occurs in other tribes.

In the Astereæ the corolla of the ray florets in *Hinterhubera* (Fig. 10, S), *Remya* and *Nidorella* is bilabiate.

The only genus in the Heliantheæ which shows normally a bilabiate corolla is *Tridax*. Here the corolla of the ray floret is of the 3 + 2 type in some species (Fig. 19, T), the two posterior lobes being distinct in *T. decumbens*, L. and very small or completely aborted in the other species, such as *T. angustifolia.* The position of this genus in the Galinsoginæ strengthens the affinity suggested (Fig. 7, Chap. II) between that sub-tribe and the Helenieæ, where the bilabiate corolla occurs occasionally in several genera.

These genera of the Helenieæ are—1, *Monolopia*, where the posterior lip takes the form of a small protuberance (Fig. 10, U). 2, *Chænactis*, where forms like those given for *Helenium* occur (see Fig. 9, 4-9). 3, *Bahia*, where the corolla is sometimes unequally and obliquely divided into four or five lobes. 4, *Microspermum*, where the outer florets have normally the 3 + 2 type of bilabiate corolla (Fig. 10, W). 5, *Pectis*, where the disc florets have the corolla sometimes unequally 5-lobed. 6, *Helenium*, (see Fig. 9, 4-9).

In all cases where there are only one or two rows of ray florets they are apt to disappear giving discoid capitula. This occurs in all tribes but especially in the Senecioneæ and Anthemideæ, see list given by Murr (62).

The Filiform Type.

The term filiform is applied to the very narrow tubular corolla (Fig. 10, A) without the expansion into a limb at the top, as in the ordinary campanulate, tubular corolla. It is more or less characteristic of the Inuleæ, which Bentham divides into two series, the first five sub-tribes with the female florets filiform, and the other four with the female florets bilabiate. This plasticity of the corolla in the outer florets in the Inuleæ is to be compared with the similar plasticity in the Cynareæ.

Outside the Inuleæ this type of corolla occurs only in *Aphantochæte, Olearia, Erigeron, Conyza, Haastia, Psiada, Adelostigma,* Baccharidinæ in the Astereæ and *Homogyne* in the Senecioneæ. In *Erigeron* the female florets are usually bilabiate and very narrow or capillary but the female florets towards the interior of the capitulum are sometimes filiform.

This filiform type is clearly another modification of the basal type, the tubular campanulate corolla. It is frequently only 2- or 3-lobed at the apex and is, therefore, considered to be derived from the basal type through the bilabiate type by an elongation of the tube and reduction in the lips. This accounts for its femaleness and its position near the margin of the capitulum and also for the transitional stages where the outer florets are bilabiate and some of the inner florets filiform.

Analysis of the Corolla Forms.

The occurrence of these various types throughout the family may be briefly summarised thus :—

Senecioneæ—Tubular, bilabiate with the posterior lip developed sometimes, filiform in *Homogyne* and palmate in anomalous cases.

Cichorieæ—Ligulate.

Calenduleæ—Tubular and bilabiate with the posterior lip developed sometimes.

Arctotideæ—ditto.

Anthemideæ—ditto, and sub-palmate in anomalous cases.

Inuleæ—Tubular, bilabiate with the posterior lip developed sometimes, and filiform in the Tarchonanthinæ, Plucheinæ, Filagininæ, Gnaphaliinæ and Angianthinæ.

Cynareæ—Tubular, bilabiate with the posterior lip developed sometimes, and sub-palmate in a number of genera.

Mutisieæ—Tubular, bilabiate with the posterior lip developed frequently, and sub-palmate in a number of genera.

Vernonieæ—Tubular, palmate in *Stokesia* and sub-palmate in *Elephantopus.*

Astereæ—Tubular, bilabiate with the posterior lip developed sometimes, filiform in the Conyzinæ, Baccharidinæ and a few other genera, and sub-palmate in several others.

Eupatorieæ—Tubular.

Heliantheæ—Tubular, bilabiate with the posterior lip developed sometimes, and sub-palmate in *Chromolepis.*

Helenieæ—Tubular, bilabilate with the posterior lip developed sometimes, especially in the Heleniinæ, and sub-palmate in several genera.

Reduction in the Corolla.

The idea that the filiform corolla is derived from the bilabiate

type receives confirmation in the tendency to complete abortion of the corolla in the female florets of several of the genera showing the filiform type, namely *Erigeron, Conyza, Haastia* (Fig. 9, 16-18), *Psiadia, Baccharis* (Astereæ), and *Gnaphalium* (Inuleæ). This tendency is also shown by *Heterothalamus* in the Astereæ, *Clibadium* and *Iva* in the Heliantheæ, *Doronicum* and *Petasites* in the Senecioneæ, and *Leria* in the Mutisieæ. Apart from their bearing on the origin of the filiform corolla, these cases serve to emphasise the tendency to reduction of the corolla material which is general in the family.

This tendency towards reduction is one of the *critical tendencies* which Wernham (90) regards as " no less important than critical characters." In considering the Campanulatæ, however, Wernham noted the tendency to aggregation of the florets and apparently concluded that reduction followed in the relation of effect to the cause (aggregation). It has been pointed out by the writer (77, p. 30) that while the tendency to aggregation may be the primary cause of reduction, the reduction would act as, at least, a partial cause in subsequent aggregation, and that there has probably been a continuous aggregation and reduction mutually interacting until the limit of efficiency has been reached.

Examples of the imperfect development of these two tendencies occur in the Lobelioideæ, Dipsaceæ, Valerianaceæ and Umbelliferæ. The development along these lines has proceeded under the pressure of orthogenesis beyond the limit of full efficiency in quite a number of Composites, such as the dense aggregations of capitula, which are frequently few flowered, in the Gundeliinæ, Angianthinæ, Relhaniinæ, Echinopsidinæ, Lychnophorinæ. Lagasceinæ and Milleriinæ. It should be noted that these specialised sub-tribes are all shown to be end groups by the structure of the pollen-presentation mechanism (see Fig. 7, Chap. II).

C. Development of the Corolla.

For an account of the development of the complete floret the reader is referred to the previous publications discussed in Section A. The differences which characterise the mature corollas arise at an early stage. The difference in development lies in the behaviour of the two posterior petals. In the tubular corolla these two petals grow at the same rate as the others and remain in organic connection, as in *Senecio* (Fig. 9, 25, 26, 27), the mature floret showing a cross section, as in Fig. 9, 19. In the ligulate corolla

these two petals grow at the same rate as the others, but the organic connection between them ceases at an early stage, as in *Taraxacum* (Fig. 9, 31, 32, 33), the mature floret showing a cross-section as in Fig. 9, 21, with the free margins of these two petals closely adpressed. In the bilabiate corolla these two petals usually fuse at an early stage and then cease to grow, as in *Calendula* (Fig. 9, 30, 29, 28) the mature floret showing a cross-section as in Fig. 9, 20, with the free margins of the two lateral petals overlapping. In this type, however, the many variations in the degree of fusion and degree of development of these two petals give the various modifications described in Section B.

The primordial meristems are free at first in all cases giving five protuberances from the top of the primordium of the flower; these meristems then fuse to give a zone which is complete in the tubular corolla, interrupted regularly between the two posterior petals in the ligulate corolla, and interrupted regularly or irregularly in the bilabiate types. The development of the filiform corolla with 2-4 teeth at the apex has yet to be elucidated.

In ontogeny, therefore, as in phylogeny, the five-lobed tubular corolla is the primitive type, and from it arises two forms more distinct in their development than in their form when mature.

Causal Morphology—Experiments have been carried out along the lines of causal morphology as suggested by Lang (47) and although more or less unsuccessful may be of interest.

Apart from an internal modification of the constitution of the organism there are two factors which may influence the production of ray florets, pressure due to crowding of the florets in the bud and variation in food supply.

Taking pressure first, this factor is not a very probable one as in the development of the capitulum the rays are differentiated from the disc before the primordia have increased sufficiently to exert a pressure upon one another (see also Church, Pt. II, p. 114). They always mature late; the primordia of the petals in the ray are undeveloped when the first row of disc florets have the corolla, stamens and gynœcium differentiated.

Experiments on the influence of pressure were made by tying twine around capitula or placing elastic bands around them so that as they expanded in the later stages of development they were subject to a pressure from within outwards in the case of the twine and partly from without towards the centre of the capitulum where

rubber bands were used.   Strong spring clips also were used to obtain pressure on two sides of the capitulum.

The material used was *Cotula coronopifolia* (a discoid species) *Ursinia speciosa*, *U. pulchra*, *Chrysanthemum Leucanthemum* (rayed species), and *Dimorphotheca pluvialis ;* this last species had given numerous capitula with bilabiate corollas in the first and second rows of disc florets.

In no case did the treatment make any difference in the development of ray florets but in a few cases of *C. Leucanthemum* tied with twine the central florets of the disc were obviously crushed and failed to mature.   The pressure in such a case arises from the expansion of the florets as it would in the case of the disc florets pressing the rays against the more or less rigid involucre.

The influence of the food supply was also investigated in *C. Leucanthemum* and *Dimorphotheca pluvialis.*   This was done by cutting a notch halfway through the stalk of the inflorescence, protecting the wound with vaseline and supporting the capitula. The results were again rather indefinite, but in the latter species the capitula so treated were rather poorly developed as a whole without much difference in the rays.   In one case, however, there were five buds in different stages above the wound and, while the other peduncles of the same plant gave numerous cases with bilabiate disc florets, none of the capitula with deficient food material showed this modification, which involves a greater expenditure of material.

These results suggest that the factor for radiateness is probably a Mendelian one (see also Trow, 84) acting directly on the production of rays and not indirectly on the food supply or the amount of pressure developed by the disc florets.   An abundance of food supply is suggested, however, as a contributary cause in the production of bilabiate disc florets and this explains, in part at least, the frequent production of " double " flowers by cultivated Composites.[1]

D.   Variation in Colour of the Corolla.

The phylogenetic value of colour as a character depends upon two chief points, our knowledge of the relation of colours and insects and our knowledge of the composition of the pigments.   In

[1] De Vries (87, p. 507) records warm weather as a factor in the production of " doubling " in the cornflower.

relation to insects all authorities are agreed that blue is the highest colour. The order of efficiency in attracting desirable insect-visitors may be taken as more or less established and beginning with green goes upwards through yellow to orange, white, pink, red, purple, violet and blue. Green, yellow, orange and white may be taken as the primitive group, and red, purple, violet and blue as advanced. The evidence as to the relative position of purple and blue was previously somewhat contradictory but the purely chemical evidence (95) serves to show that different colours, reds, blues and purples can be obtained by varying amounts of the same pigment, so that the Mendelian evidence of the duplex nature of purple is counterbalanced by the more recent additions to our knowledge of the second point.

Keeping the colour sequence in mind we can now analyse the colour of the corolla in the various groups :—

Senecioneæ—The predominant colour in this tribe is yellow, but orange, white, violet and purple occur in various groups of *Senecio*, which groups have been separated by several authors on this account. In the Senecioninæ blue occurs in *Cineraria ;* orange and purple in two or three other genera; white is rare. In the Othonninæ blue, pink and white occur rarely, while in the Tussilagininæ white and purple become relatively commoner and in the Liabinæ white is the only colour except the predominant yellow. The Senecioneæ are, therefore, primitive in the colour, showing a marked predominance of the basal yellow and a range of colour in outlying genera and outlying species of the basal genus, *Senecio*. The higher colours are usually confined to the rays, the disc in these cases being almost invariably yellow.

Cichorieæ—Yellow is again predominant, white rare, orange, pink and red commoner. There is a sudden development of purple and pure blue occurs in several genera.

Calenduleæ—Yellow is again predominant in both ray and disc florets but more so in the latter. Three of the chief genera show orange in ray and disc sometimes and two of them, *Tripteris* and *Dimorphotheca*, show white and purple occasionally, the purple spreading to the disc in both genera.

Arctotideæ—Yellow is again predominant. In the Arctotideæ the basal genus, *Ursinia*, shows yellow in both disc and ray as a rule with purple rays occasionally. This purple spreads to the disc in *Arctotheca* and *Arctotis ;* the latter shows a wide range in the rays with yellow, orange or purple in the disc. Orange occurs

in the disc of *Gazania* and purple in the rays of that genus and *Gorteria*. In the Gundeliinæ there is no yellow, only purple or violet, so that in the colour of the corolla we find confirmation of the evolution of these sub-tribes as given in Fig. 7, Chap. II.

Anthemideæ—Yellow is the predominant disc colour but white is common as a ray colour, and pink, red, purple and violet occur also. Yellow is more predominant in the Chrysanthemidinæ than in the Anthemidinæ, so that here we get the first indication of the relative position of these two sub-tribes.

Inuleæ—Yellow is the predominant colour for both disc and ray, higher colours, where they occur, frequently invade the disc. The relative positions of the Helichryseæ and Eu-gnaphalieæ are confirmed by the occurrence of white and purple in several genera of the latter, while purple is absent and white rare in the former. Blue occurs in *Printzia*, one of the Inulinæ. Yellow, orange and white are the only colours in the Buphthalminæ, the only point in which the colour of the corolla does not confirm the arrangement of these sub-tribes in Fig. 7, but see below. Yellow is dominant in the other sub-tribes but higher colours up to purple occur occasionally.

Cynareæ—Purples and blues are characteristic, a dingy yellow occurs in *Carlina* and *Atractylis* in the Carlininæ, white and blue in *Echinops ;* a distinct yellow occurs rarely in *Carduus* in the Carduinæ. These are the higher sub-tribes and in the Centaureinæ yellow occurs in *Centaurea*, *Carbenia* and *Carthamnus*, orange in the latter and in *Zoegea*. Yellow and orange are, therefore, comparatively well-developed in the sub-tribes placed at the base of the Cynareæ in Fig. 7. This fact and the predominance of yellow in the Buphthalminæ are mutually explanatory in view of the derivation of the Centaureinæ from the latter sub-tribe.

Mutisieæ—The basal sub-tribe, Nassauviinæ, shows yellow commonly in three of the chief genera, *Trixis, Nassauvia* and *Jungia*, where it is associated with the lowest type of stamen in the sub-tribe. The other genera range from yellow to blue, the latter being rare, white, pink and purple commoner. The Gerberinæ and Gochnatiinæ show a similar condition with blue absent, while yellow occurs only in *Mutisia* in the Onoseridinæ. The last sub-tribe might, therefore, be regarded as a side group with, perhaps the exception of *Mutisia*, where the yellow is associated with type IV styles and type 11 stamens. *Mutisia* would thus lead on to the Gerberinæ, giving the other genera of the Onoseridinæ as a special

development. Yellow is absent from the Barnadesiinæ, but the presence of orange in *Schlechtendahlia* confirms the primitive position as in Fig, 7, Chap. II.

Vernonieæ—Purple is predominant, with white, pink and red occasional, and yellow absent except for a greenish yellow in some species of *Corymbium* in the Vernoniinæ.

Astereæ—Yellow is again predominant in both ray and disc, especially in the latter. The chief point to be noted is the complete predominance of yellow in the Homochrominæ as contrasting with the development of a wide range of colours up to blue in the rays of the Heterochrominæ. These higher colours sometimes invade the disc, so that the relative position, as in Fig. 7, of these two sub-tribes requires to be reversed. A study of Tables VI and VII, Chap. II, shows that this can be done without inconsistency as the structure of the pollen-presentation mechanism in these two groups is very similar. The higher development of irritability (Chap. III, Sect. E) in the Heterochrominæ is also explained by this change. As yellow is predominant in the Conyzinæ and Baccharidinæ these would retain their positions as coming from the lower of the two main groups, while the Grangeinæ with purple and violet sometimes in the disc and yellow not predominant would retain its position as coming from the higher plexus. The Bellidinæ with yellow as a constant disc colour and white, or rarely blue or purple, in the ray would remain near the base of the tribe, as a side group with its present development between the main groups.

Eupatorieæ—Purple is predominant with white common. Yellow occurs only rarely in *Mikania*, which with *Eupatorium*, forms the basal group in the Ageratinæ. Pink and blue also occur in a few genera.

Helianthexe—Yellow is predominant in both ray and disc especially in the latter. All the higher colours except blue appear occasionally, white being comparatively common in the ray, but the variation is so extensive that the position of the sub-tribes cannot be distinguished.

Helenieæ—Yellow is again predominant but orange is frequent. White and purple occur but rarely in the Tagetinæ, less rarely in the Heleniinæ and Baeriinæ. Yellow is the only colour in the Flaveriinæ and Jaumeinæ, so that the position of the former is confirmed and that of the latter above the Baeriinæ is rendered

less probable. A study of Tables VI and VII shows that a lower position is possible and more data are required.

E. Anatomy of the Corolla.

For an account of the complete anatomy of the various types of florets the reader is referred to a previous publication (76) and the literature cited there. As the literature has already been discussed (Section A) it is necessary to give only a brief summary of the facts in their bearing on the general problem.

Tubular Corolla. There are five conducting strands which do not occupy the position of the midribs of the constituent petals but are situated along the fused margins (Fig. 9, 1). At or near the base of the corolla these strands, which originate in the upper distributive centre (see 76, p. 518), divide tangentially to give the staminal bundles. These pairs of bundles occupy the narrower part of the corolla, and the staminal bundles pass out into the filaments where these become free, usually at the base of the campanulate part of the corolla (cp. Fig. 9, 19).

The corolla strands continue upwards and divide radially at the bases of the corolla lobes. These half-bundles then arch over and fuse with adjacent halves, giving five arches along the margins of the five lobes. There is little or no variation in this type of corolla anatomy.

Ligulate Corolla. At the base of the corolla five strands arise from the upper distributive centre as in the above, but the behaviour of the posterior bundle is different. Near the base it divides, first tangentially to give the staminal bundle, and then immediately or a little higher up it divides radially to give two bundles which run along the margins of the ligule (cp. Fig. 9, 21 and 3). The other four bundles, some distance from the point at which they give the staminal strands, divide radially at the bases of the corolla lobes, bend over and fuse to give arches as before. The marginal bundles behave as the half bundles which they really are, and fuse with adjacent halves. The only real difference, therefore, between this and the tubular type of anatomy is that the radial division of the posterior bundle takes place earlier in the ligulate corolla. There is no recorded variation in this type of anatomy.

Bilabiate Corolla. The vascular supply of the bilabiate corolla varies with the width of the anterior lip as a rule, and the variations seem to be the result of a response to the physiological needs of

the corolla. Thus in the ray florets of *Tussilago Farfara* there are four bundles at the base of the corolla, the posterior one is short, while the two lateral strands end blindly in the tissue of the margin of the very narrow anterior lip. The one anterior bundle seems to be sufficient to supply the needs of the very narrow corolla. In the ray florets of *Calendula vulgaris* there are again four bundles, two small lateral strands occupying the margins of the anterior lip, and two larger strands occupying the fused margins of the anterior and two lateral petals (Fig. 9, 2). These form arches at the top of the corolla as in the previous types. The *Calendula* type may be taken as the usual one for a ray floret, but there are many variations. The anterior lip may be four-lobed with five bundles (two marginal), or it may be broad and three-lobed with a vascular supply for four lobes, or it may be narrow and two-lobed or entire with a vascular supply for three lobes, *i.e.*, four bundles with two marginal.

Where the anterior lip is broad the strands tend to increase in number, the accessory strands frequently developing in the positions of the midribs of the three petals, giving a total of seven. The number in the wider part of the lip is frequently increased to twelve and more by branching of the four primary strands or of the three midribs. Usually these accessory strands end blindly in the tissue of the corolla, only the primary strands fusing to form the marginal arches at the tip, but fusions of various kinds may take place.

According to a figure by Hildebrand (36, Plate V, Figs. 22-23) the vascular supply of the irregularly bilabiate corolla in *Centaurea montana* is similar to that of the tubular corolla with the radial divisions occurring at irregular heights.

The known facts are, therefore, that the anatomy of the tubular and ligulate corollas is constant, and that of the bilabiate corolla is as variable as the external form of that type.

F. Phylogenetic Significance of the Corolla.

When all the foregoing facts concerning the corolla are considered they are found to confirm the previous phyletic suggestions in all except a few points.

The primitive nature of the tubular floret, which is shown clearly by Uexküll-Gyllenband (Fig. 4, Chap. II) is confirmed by the study of the development and vascular anatomy of the corolla and the various lines of evolution shown in Fig. 4 follow comparatively closely the scheme in Fig. 7.

The distinction between the ray florets of several tribes and the bilabiate florets of the Mutisieæ is removed, making it more probable than ever that the latter tribe is a mere collection of bilabiate forms and not a natural tribe.

The occurrence of many discoid forms and the predominance of yellow in the Senecioneæ confirms that group as the basal plexus. The similarity in colour and the small change in the form and anatomy of the corolla in the Cichorieæ confirm the position of that tribe. The similarity in form and colour of the corolla in the Calenduleæ confirms the position of this tribe. The greater predominance of yellow in the Chrysanthemidinæ suggests that this is the more primitive sub-tribe in the Anthemideæ.

The colour and form of the corolla in the Vernonieæ and Arctotideæ confirm the positions of the sub-tribes in these two groups, and the yellow of *Ursinia* adds evidence for the suggestion that that genus is the primitive one in the Arctotideæ. The frequent disappearance of the ray florets in many tribes makes the origin of the Vernonieæ from a rayed group like the Liabinæ very probable, and the occurrence of several discoid genera in the Liabinæ confirms that sub-tribe as the source of the Vernonieæ. Indeed, *Gongro-thamnus*, one of the Liabinæ according to Bentham, is placed in the genus *Vernonia* by Hoffmann.

The occurrence of filiform florets in the lower sub-tribes of the Inuleæ and in a few genera of the Astereæ is accounted for by the plasticity of organisation proved for the outer florets of the capitulum. The occurrence of the same type in *Homogyne* (Tussilagininæ) shows that the tendency towards the reduc-tion of the bilabiate corolla to the filiform type is already present in the Senecioneæ, finding expression in two separate lines of evolution. The rayed condition in the higher Inuleæ may be regarded as a reversion to the general type, but it is possible that this tribe is not monophyletic but diphyletic, in which case the Cynareæ may have arisen either from the Buphthalminæ as pre-viously suggested, or from the Plucheinæ through forms such as *Cavea* (74a). Other data are required to elucidate this point.

The derivation of the Cynareæ from the Bupthalminæ is partially confirmed by the colour, yellow in a few Centaureinæ and in the parent sub-tribe. The relative positions of the sub-tribes of the Cynareæ are also confirmed by the distribution of colour in the tribe.

The derivation of the Nassauviinæ from the Senecioninæ is confirmed by the bilabiate corolla which occurs in *Brachyglottis* (cp. Fig. 10, C-D), and by the predominance of yellow in the chief genera of the former sub-tribe. The spreading of the bilabiate condition to the disc is quite homologous with the " doubling " which is of such frequent occurrence throughout the family, probably under the influence of an abundant food supply. The transition from the more or less homogeneous capitulum of the Nassauviinæ to the forms with only several outer rows of bilabiate florets is seen in the genus *Mutisia*, which also shows a transition to the higher colours. The other genera of the Onoseridinæ appear both from the form and the colour to be a special development, *Mutisia* itself giving rise to the Gerberinæ. With this change both form and colour confirm the evolution of the sub-tribes as given in Fig. 7.

In the Astereæ it is clear from the colour relations of the sub-tribes that the relative positions of the Homochrominæ and Heterochrominæ must be reversed, as suggested in Chap. III, Sect. E, the other sub-tribes remaining as they are in Fig. 7. As the degree of development of the pollen-presentation mechanism in the two sub-tribes is very similar this can be done quite conveniently without disturbing the relationships of the other sub-tribes. We then get the yellow Homochrominæ giving the Heterochrominæ with the higher colours appearing first in the rays and then spreading to the disc. The filiform corolla appears more or less sporadically and can be interpreted as the expression of a tendency to reduction which reaches its highest development in these same genera.

The spreading of the higher colours to the disc is a step towards the development of the discoid, highly coloured capitula of the Eupatorieæ, which show higher colours as a rule, yellow appearing seldom, and then only in the basal group of the tribe. The disappearance of the ray florets is a normal phenomenon throughout the family.

There is a great similarity in both form and colour in the Heliantheæ and Senecioneæ, but the higher colours are more frequent in the former tribe, thus confirming its position above the Senecioninæ. The relative positions of the sub-tribes in the Heliantheæ are neither confirmed nor refuted on account of the great variation shown in both form and colour.

The derivation of the Helenieæ from the Heliantheæ is confirmed by the similarity in form and colour, but the complete

predominance of yellow in the Jaumeinæ renders the position of that sub-tribe above the Bæriinæ less certain. It could be regarded as coming direct from the Tagetinæ.

With a few modifications, therefore, the study of the form, development, colour and vascular anatomy of the corolla confirms the phyletic lines previously suggested.

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A NEW BRITISH FRESH WATER ALGA.

By A. J. W. HORNBY, B.Sc.

[WITH FOUR FIGURES IN THE TEXT.]

THIS species of *Endoderma* was discovered in 1914 epiphytic on *Cladophora glomerata* which was attached to the sides of Rowton's Well in Sutton Park, Warwickshire. This well is very little used, and the water is very fresh and pure.

Besides being endophytic and epiphytic on *Cladophora* it was also observed on *Rhizoclonium hieroglyphicum*, but only rarely, and nothing like to the same extent did it penetrate the walls of the latter compared with the former Alga. *Chætomorpha sutoria* though present was unaffected.

The *Endoderma* is at first epiphytic on the host in the same manner as *Aphanochæte*, and then it is observed to penetrate the thick laminated cellulose walls of the host. The result is a thallus of *Endoderma*, two or three cells thick, round the branched filaments of the *Cladophora*. It is evident that the thallus is produced by the anastomosing of the branches of the *Endoderma*, closely knit together by successive laminæ of the host-wall.

The cells are at first rounded, but soon become angular by the anastomosing of the branches in all directions. They are uninucleate and differ very much in size. The diameter varies from 3·5 to 17·5μ; the average diameter is 12μ. The cell-wall is thick and quite destitute of hairs. There is one irregular parietal chloroplast, containing one, rarely more, pyrenoids, and some starch-grains. It is very dark green in colour, and apparently there is no evidence of parasitism in this plant, the *Cladophora* being unaffected to any observable extent.

Including the present species the genus *Endoderma* now contains ten species. It is proposed to call the alga under consideration *E. Cladophoræ*. Huber[1] in discussing certain members of the *Chætophoraceæ* divides his genus into two sections, those without bristles and with one pyrenoid in each cell, which he groups in the section " *Entocladia*," and those with bristles and several pyrenoids, which he groups in the section " *Ectochæte*."

The former were mostly marine, but since then three species have been discovered, which are all freshwater, and occupy a place in " *Entocladia*." They are the West Indian *E. Pithophoræ*

J. Huber, Contrib. à la conn? d. Chætophorées (Ann., Sc. Nat. 7), Ser. Botan. T. 16. Paris, 1892.

and *E. polymorpha*, described by Professor West[1] as epiphytic on a species of *Pithophora*, and the one described above. All three have much larger dimensions than the other species of this section, and it should be noted that *E. polymorpha* and *E. Cladophoræ* sometimes contain more than one pyrenoid.

Moreover, though the branches of *E. Polymoryha* do anastomose, it is only in *E. Cladophoræ* that there is the extraordinary development of thallus, leading to the formation of compact masses. This is characteristic of the " *Ectochæte* " group, Huber's three species *E. leptochæte, E. endophytum* and *E. Jadinianum*, and in the latter species, this tendency is brought to the highest point; there is often formed by the anastomosing of filaments growing away from the host-wall, a cellular colony, which frequently breaks away and is able to lead a separate existence. It is indeed the fresh-water species of *Endoderma* which have this tendency developed to the greatest extent.

The regular rounded shape, either ellipsoid, spherical or ovoid, of the cell in the young vegetative filament of *E. Cladophoræ* before the production of a thallus or penetration of the cell-wall of the host, is characteristic of this species. In all the other species, with the exception of *E. Pithophoræ*, which is further characterised by its filaments never anastomosing, the cells are very irregular and are often curiously elongated.

At present *E. Pithophoræ* seems to occupy a place by itself in this genus, but *E. polymorpha* and *E. Cladophoræ* connect up the sections " *Entocladia* " and " *Ectochæte* " of the genus *Endoderma*.

Diagnosis:—*Endoderma Cladophoræ* nov. sp.

E. epiphyticum et endophyticum; filis subbrevibus, irregulariter subramosis, ramis plerumque concretis paullo attenuatis; cellulis magnis, ovoideis vel ellipsoideis, demum e mutua pressione angularibus, chromatophoro singulo parietali irregulariter lobato, pyrenoide singulo (rarissime binis) prædito.

Long. thalli usque ad 480μ; diam. cell. 6-17·5μ; diam. cell in parte apic. ram. 3·5-4μ. *Habitat* in ramis *Cladophoræ* rarius in filis *Rhizoclonii*, Rowton's Well, Sutton Park, Warwickshire.

My thanks are due to Professor G. S. West for the supervision and assistance given in this work.

Botanical Laboratory,
  The University, Birmingham.

[1] G. S. West. West Indian Freshwater Algæ, Jour. Bot. Vol. XLII, 1904.
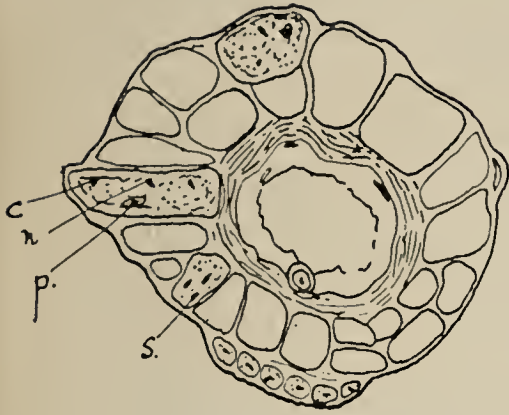
Fig. 1.

Fig. 2.
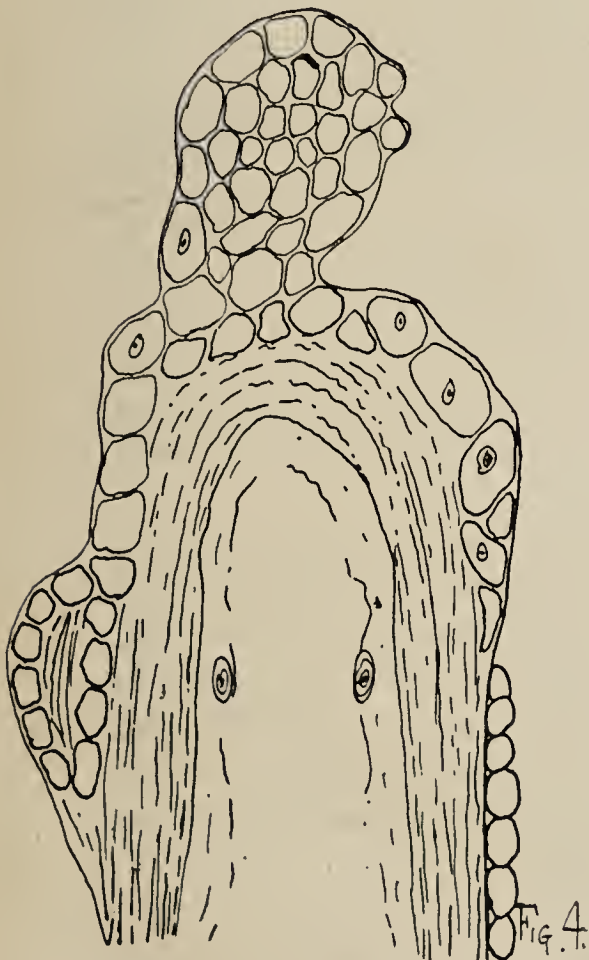
Fig. 3

Fig. 4.
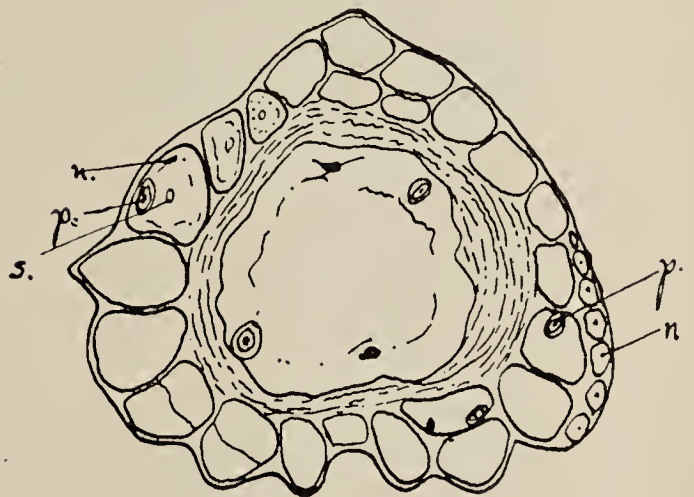
FIG. 1. Cross section of *Cladophora* showing *E. Cladophoræ*, well matured, penetrating cell-wall of host, and branches anastomosing to form compact thallus round host.

FIG. 2. Cross section of *Cladophora* showing how *E. Cladophoræ* penetrates between laminæ of cell-wall of host.

FIG. 3. This represents a further stage of process shown in Fig. 2.

FIG. 4. Longitudinal section of *Cladophora* showing terminal segment of branch. Surmounted by thallus of *E. Cladophoræ*. All figures × 540.

p=pyrenoid. *c*=chloroplast. *n*=nucleus. *s*=starch-grain.

TRANSLOCATION IN PLANT TISSUES.

IN a recent paper entitled " On the Mechanism of Translocation in Plant Tissues. An Hypothesis, with special reference to Sugar Conduction in Sieve-tubes,"[1] Mangham puts forward the view that the sugar originating inside the leaf cells travels throughout the plant "without ever passing through the plasmatic membrane, or outer surface of the protoplasm in contact with the cell wall." The path of translocation is the protoplasm, which by way of the connecting threads between individual cells and the protoplasmic lining of the sieve-tubes is continuous over the whole plant.

The paper in question is stated to be the outcome of an attempt to form some mental picture in terms of physical chemistry, but certain of the physico-chemical statements upon which this hypothesis rests cannot be accepted as correct.

The main features of the hypothesis can be best indicated by extracting from the summary appended to the paper. " It is suggested that in vegetable protoplasm there are present constituents capable of absorbing sugars from solution. For any given concentration of sugar present in the liquid phase of the protoplasm and the cell sap continuous with it, there would be a definite concentration of sugar present at the absorbing surface. Any alteration of concentraction in either region would lead to a re-adjustment of concentration equilibrium, *which would be propagated as a wave through the system. . . . . The rate of propagation of this wave would depend very much upon the degree of approximation of the adsorbing particles . . . .*

From the statements which have been italicised here it appears to the writer that Mangham's mental picture is founded on fallacious physico-chemical concepts. Mangham considers that, if the absorbing particles were far apart, the " rate of movement of sugar would be conditioned . . . . by the rate of diffusion; but, if the absorbing particles closely approximate, the rate of transference would then approach "that at which condensation on the surface of the absorbing phase would occur . . . . it would be extremely rapid." Bayliss, *Principles of General Physiology,* pp. 56 and 61 is cited, but I have been unable to find under the reference any support for these statements. Bayliss rather appears to state clearly that while the actual process of attachment occurring when a substance *reaches* a surface at which it is

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[1] Annals of Botany, 1917, 31, 293-311.

absorbed, is probably one of very great rapidity, the movement of such substances is always controlled by the laws of diffusion. Mangham, however, speaks of an "*adsorptive suction.*"

With regard to Mangham's "wave" concept, I must confess to having experienced some difficulty in arriving at a point of view from which this mental picture is comprehensible. It appears to have had its origin in the application of a false analogy. Mangham states that "a wave of disturbance and readjustment of equilibrium is propagated, in much the same way as the firing of shells from a battery leads to the depletion of the immediate supply, followed by a replenishing from the reserves, etc., and ultimately from the factory, so that the scheduled relations are maintained between the various stores at intermediate points." It is clear that in this picture, which involves the intervention of human activity in the replenishing of reserve dumps successively from the rear, the conception of a wave is not altogether inapplicable. Nevertheless, if the shells represent sugar molecules and the dumping spots absorbing particles, its use as an analogy is entirely false and misleading. It obviously involves a diffusion of sugar against the diffusion gradient.

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THE OSAZONE METHOD FOR DETECTING SUGARS IN PLANT TISSUES.

IN a recent number of this journal, S. Mangham offers some explanations of his earlier writings on the osazone method for detecting sugars in plant tissues. In the course of his note he calls attention to a passing reference made by us in regard to the detection of sugars in which we said "The fact that Mangham should claim to distinguish between *d*-glucose and *d*-fructose in the plant by the osazone test, when their phenyl osazones are of course identical, is not very reassuring as to the degree of reliability of his results."

Mangham is in error in reading into this statement an assumption that he considers a chemical difference to exist between the phenyl osazones yielded by glucose and fructose. These sugars yield the same phenyl osazone. Many chemists feel sceptical of microchemical tests applied to plant tissue and would only fall

back on them when others are not available. Further, the osazone tests are of doubtful applicability in the case of mixtures of sugars. Such mixtures are present in plant cells. For these reasons we felt and still feel that a claim (even if it is only a half claim) to distinguish between two sugars in plant tissue by means of the osazone test, when the two sugars yield the same osazone, is not very reassuring as to the degree of reliability of the results obtained, even if there is "a question of the influence of viscosity upon molecular rearrangements, diffusion and crystal formation," which results in the formation of different crystal aggregates.

Nevertheless, readers might be excused for drawing from the section of Mangham's paper headed "Effects of Glycerine" the conclusion that Mangham considered glucose and fructose to yield different osazones, for he speaks of "dextrose and levulose phenyl osazones," "the two osazones," "the osazones." Above all the description of Experiment III, in which "levulose and dextrose phenyl osazones were added to pure glycerine" and the behaviour of the resulting mixtures of osazone and glycerine compared, seems to assume the existence of two osazones, and the experiment appears to have for its object a determination of different properties of the two. In our opinion the use of the expression "two osazones" in Mangham's paper for different forms of crystal aggregate of the same osazone is liable to misinterpretation, just as Mangham's use of the symbols '*d*', '*l*' and '*dl*' to represent the types of osazone crystal aggregates yielded by glucose, fructose and sucrose respectively, does not conduce to clearness of thought when the symbols *d*, *l* and *dl* have a universally accepted and quite different signification in sugar chemistry.

However, as Mangham has now made his position clear, further discussion is unnecessary. With his conclusion that Senft's reagent cannot be used to distinguish with certainty the individual sugars of a mixture we certainly agree. With regard to his further conclusion that this reagent is of considerable value in certain forms of research we feel some scepticism; it is a nice question whether it is ever worth while employing a bad method that can at best only give questionable results "indicating probabilities rather than as affording demonstrations." It appears to us that in many cases the result would be the expenditure of time in accumulating data of little value, accompanied by what is perhaps worse, a tendency to accept "probabilities" as facts.

INGVAR JÖRGENSEN.

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THE NATIONAL UNION OF SCIENTIFIC WORKERS.

To the Editor of the NEW PHYTOLOGIST.

Dear Sir,

I have read with interest your carefully written editorial in the Jan. and Feb. issue of the NEW PHYTOLOGIST dealing with the National Union of Scientific Workers. I must say at once that there are many who will appreciate your belief that any proposal for the establishment of a national organisation of men and women of science has a *prima facie* claim on the very serious attention of all scientific workers and that the formation of an association having the functions of a trade union may be necessary. I am not clear, however, why you should regard as likely to incur censure among influential men the fact that the National Union of Scientific Workers appears likely to insist among its aims when they are *finally* formulated on "the promotion by corporate action the economic interests of its members." You yourself, Sir, appear in the preceding number of the NEW PHYTOLOGIST as one of the authors of a memorandum dealing with "The Reconstruction of Botanical Teaching" in which it is stated that your object is to put forward five concrete proposals, the fifth of which reads as follows :—

"A determined and general effort should be made to raise the remuneration of teachers and of holders of purely research posts to a reasonable living wage."

In the present number "Witness" cordially agrees with the remarks of the authors of this memorandum on the pressing need for reform in this matter (the scale of payment to Botanists). Surely "Witness" and also the five signatories of the memorandum including yourself, Sir, are to be regarded as "influential men," but if they are among those who, as you say, "are exceeding unlikely to approve the formation of a Union" it cannot be for the reason you think, namely, that its aims were provisionally stated to be the promotion by corporate action of the economic interests of its members.

To return, Sir, to your own remark about the National Union, I agree thoroughly with you that the interests of science and of scientific work would seem to deserve at least an equal place with the economic interests of its members in the programme of a union of scientific workers and that there appears to be no insuperable difficulty in combining the two classes of aims. But I think that in formally interpreting the provisional resolutions passed by the body which elected the committee to proceed as they think fit with the formation of the union, you have missed the point that they are so combined in the programme of the National Union of Scientific Workers as outlined by that committee in its pamphlet issued in January last, with which you dealt. The following lines of action are therein suggested among others:— " To seek representation on public committees considering scientific reconstruction; to unify and support energetically all schemes for improving scientific education; to conduct educational propaganda on the importance of scientific research in the national life; to set up a permanent committee to propose, support and oppose new legislation in connection with other bodies ; to conduct a journal, etc." It is quite clear that these are matters affecting " the interests of science and of scientific work " as distinguished by you from the economic interests of the workers.

You say in another place that the proposed union, judged by the declared aims of its promoters appears "to have its place rather in the world of labour." This statement applies correctly enough to such a body as the Association of University Lecturers, but it does not appear to march so well with the character and objects of the National Union of Scientific Workers.

It appears that there is some urgency in the interests of national efficiency and scientific efficiency for the scientific community to get together and organise itself. A revolution in the scientific world is practically necessary. It must be either towards a thoroughly bureaucratic system, or towards a thoroughly democratic one. If bureaucratic, then let there be an authority *to choose the bureaucrats for efficiency and for efficiency only.* Otherwise the organisation achieved will be worthless. It is doubtful whether there can be such an authority in this country. If democratic, organisation is none the less vital. Its success, and therefore the success of science, turns upon the capacity for individual and sectional accommodation and sacrifice, which is only possible on the basis of a large-minded spirit of compromise in the interests of the whole. The National Union will clearly stand opposed to any development

towards German bureaucracy in science. At the same time there is obviously involved in its adoption, the acceptance of a measure of discipline. I myself regard the " economic interests" plank in the programme of the National Union as a very fair test of individual motive.

<div align="center">

I am, Sir,

Yours, etc.,

</div>

St. John's College,   FRANKLIN KIDD.

<div align="center">

Cambridge.

</div>

29th March, 1918.

<div align="center">

To the Editor of the New Phytologist.

</div>

Dear Sir,

The editorial statements on the above subject in the last number of the New Phytologist appear to arise from a serious misunderstanding of the objects of the Union. At the two preliminary meetings in London at which it was decided to form an organisation, the supporters of the resolution defining the aims of the Union as " the promotion by corporate action of the economic interests of its members " held that the word " economic " was to be interpreted in the widest possible sense. There was considerable discussion on the question whether the phrasing actually adopted was the best to indicate the views of the meeting ; but the general attitude on the more important question of the desirability of including aims that could not be regarded as economic in the narrow sense that you seem to have adopted, can be judged from the fact that of the eight persons elected to the executive committee not one favours the application of the word " economic " in this sense.

I fail to understand the motive for some of the remarks in your note. You agree that a national organisation of scientific workers, on a democratic basis, and combining economic objects with the promotion of the interests of science and of scientific work, would be a desirable thing ; yet when a body of precisely this character is formed you ignore several essential statements of the organisers and describe as an emphasising remark that " economic questions must always be the primary concern of the association," whereas with its proper context it gives the reverse of emphasis.

Certain aims not definitely economic are specifically set forth in the circular : " To unify and support energetically all schemes for improving scientific education : to conduct educational propa-

ganda on the importance of scientific research in the national life ; to set up a permanent committee to propose, support, or oppose new legislation in conjunction with other bodies." The committee were unanimous on these objects after detailed discussion, but as they did not wish the Union to be permanently pledged to a definite programme by so unrepresentative a body they stated them with some reserve. Because they did this it is hardly fair to refer to their statement of aims as " a suggested ' hinterland ' of other objects, as yet undetermined."

With your statement that " no one can avoid judging of the desirability or otherwise of a proposed organisation by the declared aims of its promoters " I cordially agree, provided *all* the aims are considered. I hope, therefore, that in order to correct the bad impression that may have been created in certain quarters by your omission of some of our most important statements you will consent to give to this note the same publicity as to your own.

Yours sincerely,

HAROLD JEFFREYS.

[We are glad to print the letters of Dr. Kidd and Dr. Jeffreys because between them they give a clearer insight into the real aims of the Executive Committee of the National Union than was provided by the circular on which we commented. The object of that comment was to warn the promoters that they could not remove the impression created by the unequivocal statements on the first page by referring on the second to "the suggestions made of methods by which the Union might seek to attain its aims," admirable and far-reaching as many of these suggestions are. You cannot destroy the plain meaning of such a resolution as " That the aims of the Union be the promotion by corporate action of the economic interests of its members," emphasised by the remark that "economic questions must always be the primary concern of the association," by adding that " other and easily definable interests must not, of course, be neglected," or by proceeding to define these interests in the form of suggestions for methods by which the Union might seek to attain its aims. Nor is it of any use to explain later, as Dr. Jeffreys does in his letter, that the members of the Executive Committee do not " favour the application of the word ' economic ' " in what is, after all, the sense in which most people understand it, and in which, too, it seems to be used in the last paragraph but one on the first page of the circular.

It may be safely stated, we think, that no National Union will meet with anything like general acceptance and support among scientific men unless the interests of science itself are at least co-ordinated with the interests of the workers in any formulation of aims. We should, indeed, have thought it sounder, both in logic and policy, to put the interests of science first, and then go on to explain that science can never take its proper place in national life unless the economic interests of the workers are secured. That proposition is perfectly susceptible of convincing demonstration, and is no doubt very readily ignored by those who have the good fortune to be financially comfortable, and who are mostly the same as the people of influence. If, without impertinence, we may offer a further word of advice, it is this. Do not trust to a General Meeting to define " with precision " "the aims and policy " of the Union. If you do you will be disappointed, either in the precision or in the aims and policy adopted, or in both. Get together a body of people who have certain ideas in common, which they believe to be sound and to be of urgent importance, state those ideas and how you think they should be carried into effect with the greatest care and precision of which you are capable, and then seek the support of all those whose interests, whatever they may be, lie within the sphere of the ideas. If you must have the support of the whole body of men and women of science see that the ideas are so stated that they will appeal to the whole body.—EDITOR].

THE RECONSTRUCTION OF ELEMENTARY BOTANICAL TEACHING.

To the Editor of the NEW PHYTOLOGIST.

ECOLOGY AS A SUBJECT FOR TEACHING.

DEAR SIR,

Being a physicist with only an amateur's interest in botany, and having never had the fortune, good or bad, of experiencing elementary botanical teaching, I must commence by apologising for my intrusion into a purely botanical discussion. With much that has been said on this subject I am in hearty agreement, but I view with alarm the suggestion that ecology, in its present state, should form part of elementary courses. The objects of teaching are firstly, to train the student to think, and secondly, to impart information. Opinions differ as to which of these is the more important; both are unpleasant processes, the former being the more so from the teacher's point of view. Now on both grounds ecology seems to me to be in an unsuitable state for teaching purposes. In most subjects knowledge comes by the gradual accumulation of research; after a suitable delay it is incorporated into text-books and courses of lectures. By this time it has been adequately criticised and the teacher has an opportunity of giving an account both of the present position of his subject and of the steps that have led to it, thus achieving both objects. Ecology is in the unfortunate position of a subject where the text-books are considerably in advance of research. Plants have been classified in detail according to their water relations and the soluble and insoluble constituents of their soils; they have been reclassified according to morphological characters believed to be of ecological importance; and when the two classifications have not at first coincided the differences have been removed by the invention of many new words. Yet the specific instances where the cause of the relation between two plant-communities has been conclusively traced are very few; they certainly do not reach three figures, and barely two. The remainder of ecology at present is description and speculation unsupported by experimental evidence. Now in the first place what training in connected thought can an elementary student gain from such a subject? All the steps of all the reasoning that has yet led to discoveries in it could be given in a

single lecture. After that the teacher would be reduced to the mere descriptive part, of which there is a vast quantity, and which can be understood without any thought at all, and to the speculative part. How he would deal with the last depends on his individual temperament. Some would state the dogmas as facts and insist on their accurate reproduction in the examination room ; the intellectual powers of few students would stand such a strain. Others would state them with much reserve, but the reservations and qualifications would be so numerous that listening to the lecture would be intolerable, and the average elementary student's touching faith in the omniscience of his or her teacher would be seriously disturbed. The most satisfactory solution would probably be to drop the dogmas altogether and convert the course into a series of interesting magic lantern entertainments. The residual effect on the mind would probably be zero, but this is the best result that could be expected.

There remains the question of the conveyance of information. This means an insistence on the descriptive part of the subject, which is an important scientific work in itself, ranking with stratigraphical geology. A difficulty must, however, not be over-looked. Associations are mainly specified by their dominants, and most dominants in this country are grasses and sedges. Often, as in the case of *Agrostis vulgaris* and *A. alba,* a wide ecological difference is associated with minute external characters. To distinguish associations a sound knowledge of these groups is therefore necessary, and this implies an extensive field training. To make even the rudiments intelligible to the average student would take at least two summers, the first being for the most part devoted to the task of learning to recognise the easier dicotyledons. After this ecology could profitably be taught, but by that time the student would be in his third year and regarded by most people as beyond the elementary stage. Thus in any case it seems impossible to include ecology as a set subject in an elementary course, though an increased amount of field botany might well be taught and certain ecological ideas imparted in connection with other subjects. I understand, however, that the last is done already.

In an advanced course the matter is quite different. The student is already prepared with enough knowledge to appreciate the differences between the plants considered, and can glean suggestions for research at every point of the descriptive part of the subject. Then ecology can be taught with profit. When

research is undertaken another reform is needed. Most universities require their lecturers and non-graduate students to reside most of their time, which makes it impossible for them to carry on ecological research more than half a day's journey away. Thus areas not close to a university town can only be treated ecologically under great difficulties. To make an improvement in this respect it is necessary that researchers shall not be compelled to reside during the summer and shall have a considerable amount of free time in the winter. Then real knowledge in ecology will grow rapidly and in time reach sufficient magnitude to be included without injury in an elementary course.

<div align="center">Yours sincerely,
HAROLD JEFFREYS.</div>

[We had not intended to comment upon points raised in this discussion until its close, but in view especially of Dr. Jeffreys' letter it seems desirable at once to try to prevent further misunderstanding on one or two points. We are in close agreement with many of Dr. Jeffreys' contentions. Emphatically ecology is *not* in a state of development which fits it to be included " as a set subject in an elementary course." We do not believe in " set subjects " at all in elementary courses of botany. We believe rather in presenting a selection of material from the whole range of our knowledge of plants which will enable the student to form a picture of plants as living organisms of definite structure and definite physical and chemical constitution conditioned by their physical, chemical, and biotic environments—not primarily as structural forms to be brought into phylogenetic relation with other structural forms, nor even as machines in the sense of structures the parts of which are adapted to perform work for the benefit of the whole. Both those points of view have their justification and their uses, but exclusive insistence on either or both gives the student a bias which is relatively sterile in its results. We do not think it is open to dispute by those acquainted with the subject that the field of ecology provides essential material for the selection suggested. It is obvious that in mere bulk a description of facts of structure is bound to preponderate in any course on elementary botany. But " Witness " is of course entirely right when he says that " the mere description of the parts of which plants are composed is necessarily dull and without any obvious bearing on general problems." The question is, what are the general problems to which the attention of elementary students should be directed? Not, we submit, phylogenetic problems, nor quasi-artificial teleological problems.—EDITOR.]

A PLEA FOR FREEDOM.

Sir,

I would like to urge upon your notice one or two considerations which influence me in witholding agreement from your most note-worthy proposals about the reform of botanical teaching, in their present state.

Firstly, and most broadly, I object to revolutions, for I cannot see any guarantee either in history or in logic for their efficacy. The normal always re-establishes itself.

Secondly, I think the premises of the memorandum are wrong. Morphological botany has not failed, so far as I can see, to justify its primordial claim to be the elementary basis of the science ; since I maintain that the sensuous impressions of morphology are more easily apprehended by the outsider, either layman or young student, and, on the other hand, its subtle and mysterious speculations have a semi-religious fascination over him, more than anything in cold and formal chemico-physical analyses, marvellous and truthful though these are.

Again, *within the limits* of my own experience, students who are attracted to the science at all are more easily inclined towards a liking for morphology, even by an indifferent teacher, than towards physiology, even by a teacher with personality. I know of no enthusiasm among physiologists to compare with the brilliant and heart-felt devotion to morphological and systematic botany among the men I have known. Maybe these points are simply the expressions of a weakness of the human mind for the tangible rather than the abstract, but surely it is this very weakness that must be most carefully taken into account in deciding what is to form the introductory phases of the science in our classes.

There is another aspect of these proposals, which may not have struck those responsible for them, and that is the intense distaste which now reigns almost everywhere for the prospect of fresh upheavals after the war. If there is one thing which every single man, apart from a few red-souled plotters, longs for, it is to be let alone in peace after the war to work out his destiny in his own way.

No more shifting and turmoil, no more bullying and dictation ! It is *peace* we want, really peace, in every phase of life. Every attempt to enthrone this grey-faced efficiency, every attempt to key up the struggle to infinite lengths beyond the duration of the war,

preaching future subjection to German methods of universal interference and control, is running counter to this instinct. Moreover, it is helping to win the battle for prussianism.

Changes there must be, no doubt, but any effort at a universal disturbance which would destroy all the old landmarks, is going to arouse most rancorous animosity.

I must admit I take up the position which you condemn. I *do* say let there be more physiology taught and I do *not* say let there be nothing taught but physiology. One-sided exclusion is foolish in every direction, but personal acquaintance with some of the advanced men on both sides leaves me in no doubt as to the side on which exclusiveness is lauded as a virtue, and on which it is justly condemned as a vice. Among those who take the former view, there are, I fear, bigots who would make it hardly possible for a morphologist to survive. If those who have signed the memorandum have their way the new methods will play straight into their hands. Morphology is to be driven into a corner, and allowed one school in three. Instead of the recognised basis of the science it will become the mere adjunct of physiology. Under such a tripartite system no man could, but by chance, follow the line that nature directs him to. He would be bound to accommodate himself, perforce, to the scope of the school that is open to him for a livelihood—a neat system, in fact, for the manufacture of square pegs.

Those who may raise the specious demand "to bring botany into closer touch with reality" are between a warp and woof of error. In one direction they plainly limit themselves to the most unphilosophical aspects of the theory of reality, while in the other direction they become committed to wholesale interference with the development of their colleagues' abilities where these do not coincide with their own prescribed ideas.

Well, I champion the cause of freedom! I would claim and defend the right of every botanist to think and practise according to his own beliefs without hindrance. The only liberty I would deny to any man is the liberty to dictate to his neighbour's conscience. Away with the imposition of scheduled uniformity, it is the bane and shroud of intellect! Let us all have peace and amity, and freedom, in heaven's name, to do as we think fit.

I would suggest as a counter to the proposed move, something more in accord with evolutionary principles, namely, *the abandonment of restrictive schedules in all grades*, so that every man may be free to teach according to his lights; while as a corollary,

examination papers should be divided into sections of equal value, in any one of which a student may satisfy the examiners, according to his personal bias. Naturally a much higher standard could thus be demanded from a student in each particular section, while a direct encouragement would be given to originality and talent in the teacher, which might result in definitely characterised schools, on the antique model, springing up, based on the personality of their greatest teacher and moulded by his tradition, but retaining their plasticity. This is simply a return to a more primitive ordering of affairs, calculated to prevent the danger of schism, since that is in inverse proportion to the elasticity of the bonds holding a community together, and also allowing unfettered power of development to those who reject the present order.

Rigid control and forced systematization are the greatest errors in science and art, or indeed in any of the manifestations of that essentially irregular creature, man. I am all for diversity. I can never consent to a dragooned uniformity on one side or the other. I support with all my heart the cause of compromise and rational balance, but I condemn with abhorrence the demand of any one section of opinion to impose its limitations upon the whole body of the science.

I am, Sir,

Yours, etc.,

R. C. McLEAN.

SOME OBSERVATIONS ON THE BEHAVIOUR OF TURGESCENT TISSUE IN SOLUTIONS OF CANE SUGAR AND OF CERTAIN TOXIC SUBSTANCES.

By D. Thoday, M.A. (Cambridge).

[With Eight Figures in the Text]

THE experiments described in this paper were made several years ago in the course of investigations on the effect of anæsthetics and other toxic substances on respiration. They were suggested by A. J. Brown's remarkable observations on the selective permeability of the coat of the barley grain and the influence of different solutes on the rate of entry of water into the grain.[1] Pieces of potato were put into various solutions and their gain or loss in weight followed in order to see whether the behaviour of this very different material corresponded with that of barley grains in solutions of the same substances.

The structure of the material made the problem a more complicated one than that which Brown was investigating. In the case of the barley grain the whole grain forms a single "cell," enclosed in a membrane which is chemically and mechanically very resistant. Brown and his collaborators have therefore been able to formulate their problems in relatively simple terms, viewing the dry seed "as a diffusion system consisting of a mass of solid material capable of absorbing moisture enclosed within a differentially permeable membrane."[2]

Lately they have summed up their earlier work as follows: "Previous results . . . have demonstrated that when seeds of *Hordeum* are immersed in solutions of solutes to which the seeds are impermeable, less water enters the seeds than from pure water, and that the actual amount entering is regulated, in the main, by the osmotic pressure of the solution in which the seeds are immersed . . . On the other hand . . . that with solutions of those solutes which are able to diffuse through the seed membrane there is a general tendency not only for more moisture to enter the seeds than from pure water itself, but also for the rate of entry of the moisture to be accelerated to an extent varying with both the nature of the solute and the concentration of its solution."[3]

The outstanding questions clearly relate to the causes which determine on the one hand the degree of permeability of the

[1] Proc. Roy. Soc., B. 81, 1909, p. 82.

[2] Brown and Tinker, Proc. Roy. Soc., B 89, 1915, p. 119.

[3] *Loc. cit.*, 1915, pp. 119-20.

membrane to particular solutes, and on the other the increased rate of entry and final percentage of water in their presence. Recent work has led them to lay stress on the correlation between both these effects and the lowering of the surface tension of water brought about by those substances in solution which penetrate the coat.[1]

In potato parenchyma the first and most important complication lies in the complex nature and chemical instability of the chief differentially permeable membrane present, the protoplasm. The water content of the vacuolated cells is, moreover, considerable, so that the entry of water is more an osmotic phenomenon than an imbibitional swelling of colloids, although such swelling—of starch as well as cellulose and proteids—must occur. It has also to be remembered that the turgescent condition of the tissues introduces from the very beginning of the experiment what Brown and Tinker call a "backward pressure" retarding the entry of water. In addition, the presence of air-spaces introduces a possible source of error, especially in dealing with substances that lower considerably the surface tension of water in contact with air ; for solutions of these substances might, by virtue of this very property, tend to inject the air-spaces and so cause an immediate increase in weight, as well as a more rapid subsequent entry owing to the larger number of cells brought into direct contact with the solution.

In view of such considerations, although the results obtained were interesting, some of them curious, they were put on one side, as further work would have led away from the track of the main problems under investigation at the time. No opportunity of following them up with more critical experiments has since occurred; but, in view of the recent appearance of a paper by Stiles and Jörgensen[2] describing promising preliminary work[3] along the same lines, it seems an opportune moment to make the chief results available.

1. Experimental Results.

The method used was cruder than that elaborated by Stiles and Jörgensen. Nevertheless the errors of manipulation and weighing were small, and errors of sampling do not seriously affect the form of the individual curves : while even a rough quantitative

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[1] *Loc. cit.* ; also Proc. Roy. Soc., B 89, p. 373.

[2] " Studies in Permeability, V." Annals of Botany, XXXI, 1917, p. 415.

[3] The curves given in their Fig. 4 (*loc. cit.*, p. 422), showing the different behaviour of pieces of potato in distilled water at various temperatures, are a particularly encouraging example of what can be done by this method, used with care and discrimination.

comparison is legitimate between curves obtained in the same experiment with material from the same tuber.

Adjacent rectangular pieces of approximately the same size and shape, or cylindrical pieces of equal length were cut from the interior of a tuber, blotted, weighed, put into water or solutions, and thereafter blotted and weighed at intervals. The initial weight of the pieces taken was in most cases between 4 and 5 grammes.

All the results have been calculated as percentages of the initial weights and plotted against the time. In a final analysis, however, it would be a point for consideration whether unit weight or unit surface area would be the more satisfactory basis.[1] The method of Stiles and Jörgensen has the advantage that, in addition to reducing the sampling error, it secures a close approximation to equality both of weight and of surface.

Limits of Error. The results given in the following table show the degree of correspondence obtained when similar pieces of tissue were treated in the same way. The data are those on which Fig. 3 is based, confirming a result with M/100 mercuric chloride solution to be mentioned later.

Initial weight in grms.	Gain in weight in gms.			Percentage gain in weight.		
	30 mins.	63 mins.	93 mins.	30 mins.	63 mins.	93 mins.
In distilled water.						
2·579	0·078	0·142	0·172	3·0	5·5	6·7
2·580	0·090	0.154	0·190	3·5	6·0	7·4
2·561	0·085	0·147	0·188	3·3	5·7	7·3
2·600	0·089	0·164	0·210	3·4	6·3	8·1
Mean ± probable error				3·3±0·1	5 9±0·1	7·4±0·2
Maximum difference from mean ...				0·3	0·4	0·7
In M/100 mercuric chloride.						
2·620	0·093	0·123	0·121	3·5	4·7	4·6
2·526	0·094	0·132	0·133	3·7	5·1	5·2
2·580	0·110	0·143	0·146	4·3	5·5	5·7
2·631	0·116	0·151	0·153	4·4	5·7	5·8
Mean ± probable error				4·0±0·2	5·2±0·2	5·3±0·2
Maximum difference from mean ...				0·5	0·5	0·7

Cane Sugar.

Experiments were first made with various concentrations of cane sugar, to obtain curves illustrating the simple osmotic entry or

[1] Cf. Stiles and Jörgensen's discussion of this question and their test experiments, in connexion with the exosmosis of electrolytes. "Studies in Permeability IV," Annals of Botany, XXXI, 1917, pp. 52-3.

withdrawal of water. Those given in Fig. 1 are essentially similar to Stiles and Jörgensen's curves for the same substance (*l.c.*, p. 425, Fig. 7).

Hours of immersion.
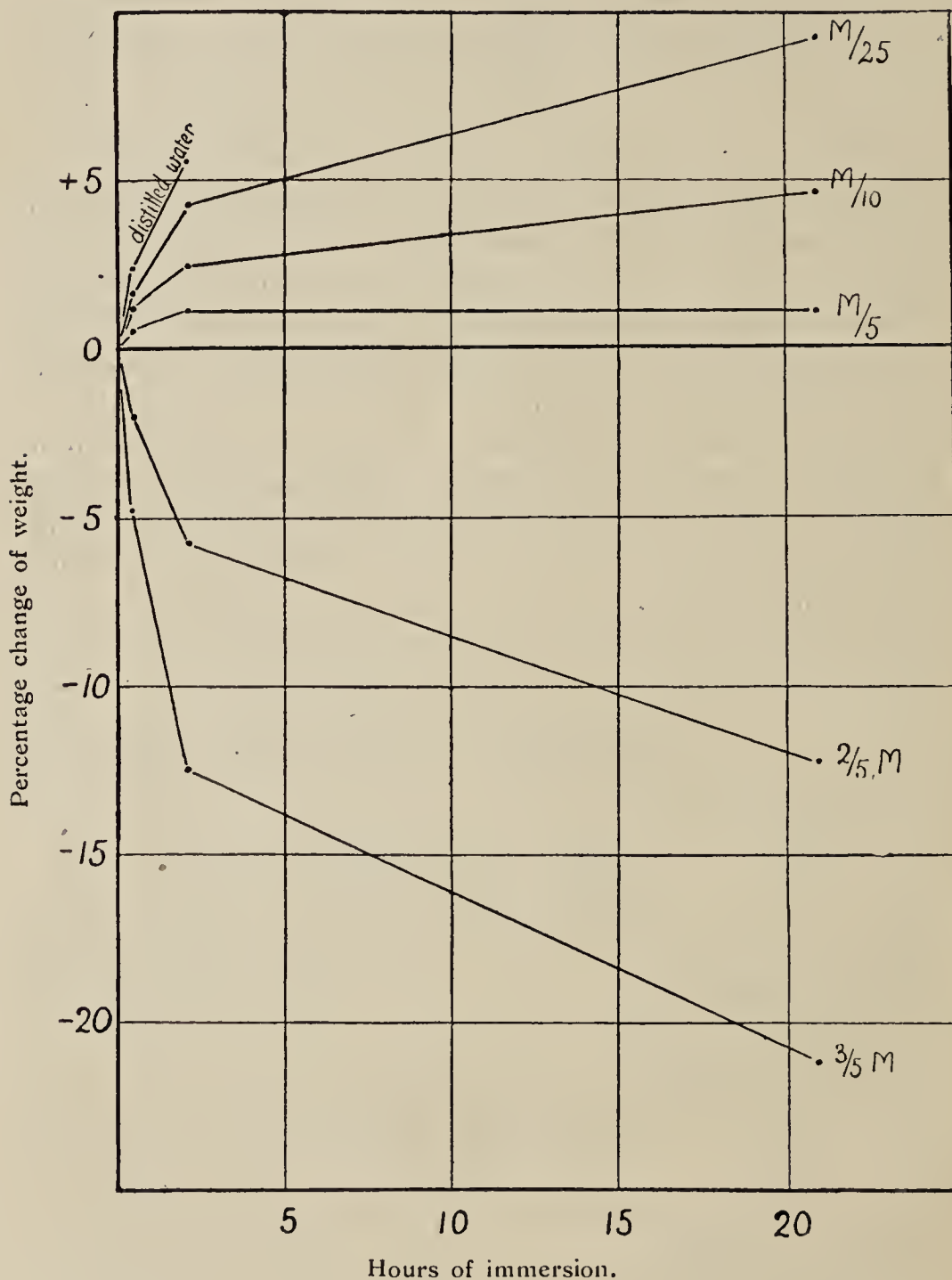
Fig. 1. Cane sugar.

They indicate that the pieces of tissue were initially in a condition of turgescence such that they would have been in equilibrium[1] with a solution rather stronger than M/5. The curve

[1] Stiles and Jörgensen describe such an equilibrium by saying that " the solution was approximately isotonic on the osmotic hypothesis with the cell sap." ("Studies in Permeability V," p. 425 ; also p. 426). This statement is misleading and is founded on a prevalent misconception which will be discussed in a subsequent paper.

for this strength indicates that a relatively stable condition of equilibrium was soon reached which could persist for at least 20 hours. It would appear that the protoplasm maintained itself in a condition approaching closely to perfect semipermeability as regards both the sucrose and the solutes of the sap.

Toxic Substances.

Mercuric chloride. These results (Fig. 2) are curious in that the solutions entered at first apparently faster than distilled water—
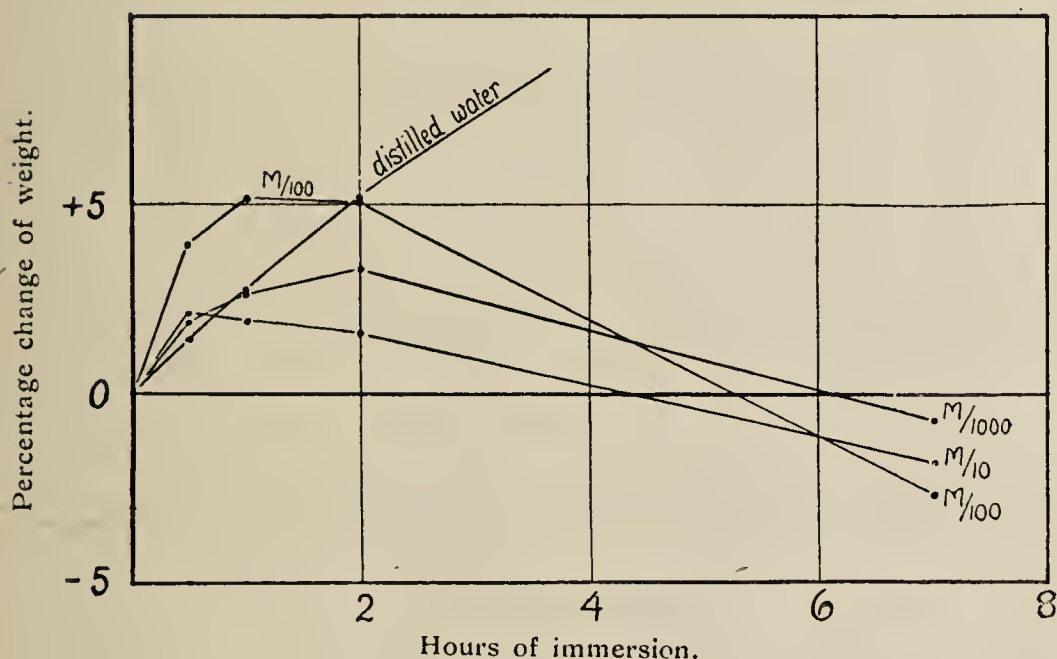
FIG. 2. Mercuric chloride.

a quantitative result which was fully confirmed for the M/100 solution by other experiments. The curves given in Fig. 3, for example, represent in each case the average of four sets of observations, the pieces used being taken from the same tuber.

The most rapid entry occurred in the case of the M/100 solution. Slices cut from a piece at the end of 7 hours in this solution, tested with ammonium sulphide, showed that mercuric chloride had penetrated to a depth of 3 or 4 mm. In another experiment, after half-an-hour the depth of penetration was only about one millimetre ; yet the gain in weight in this short period was 4% as against 2% in distilled water. It is unlikely, therefore, that the weight of absorbed mercuric chloride accounts for more than a fraction of the difference.

Another possibility remains to be excluded before the result can be interpreted as truly an effect of the mercuric chloride on the entry of water into the cells—namely, the injection of the air-spaces, which has already been mentioned as a source of error. No data appear to be available on the effect of this salt in solution

Hours of immersion.
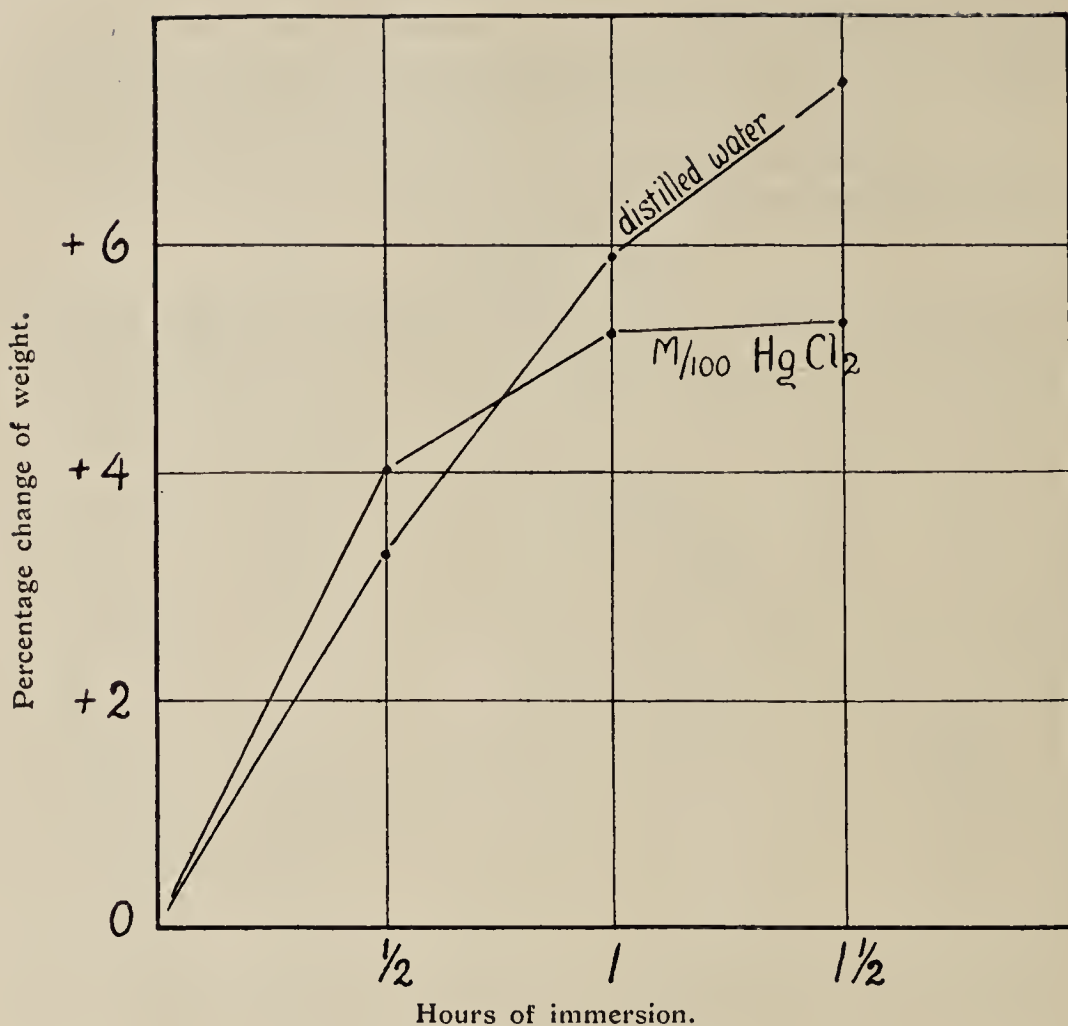
FIG. 3.　Mercuric chloride.

on the surface tension, but a rough test with capillary tubes showed
no appreciable difference of capillary rise as between the M/100
solution and distilled water.　Observations on the changes in total
volume of pieces of potato and the liquid in which they were
immersed showed a small decrease, indicating some injection, but
no significant difference between an M/100 solution and water.

In order to settle the question, experiments have been made
recently in which pieces of potato were injected under the air-
pump.

In some of these experiments one lot was injected with water,
the other with the solution.　In these the greater increase in weight
was demonstrated only in the first period which included the actual
injection.

In others both lots were injected with water, and then immersed
in M/100 H_gCl_2 and distilled water respectively.　In these the
ncrease of weight was always much greater in the solution during
the first quarter-of-an-hour.　The following data are taken from one
of these experiments :

Ten slices about 3mm. thick were cut from a tuber, a disc about 3½ cms. in diameter was punched from each, all the discs were rapidly rinsed in tap water, and then were transferred to distilled water under an air pump. After five minutes under reduced pressure they were injected, divided into 2 lots, blotted and weighed and put into M/100 mercuric chloride and distilled water respectively.

M/100 Mercuric chloride.			Distilled water.		
Initial weight, 17·16 grammes.			Initial weight, 17·58 grammes.		
Minutes of Immersion.	Gain in grammes.	Rate of gain % per hour.	Minutes of Immersion.	Gain in grammes.	Rate of gain % per hour.
15	0·78	18·2	16	0·52	11·1
15	0·14	3·3	14	0·20	4·9
23	0·04	0·6	24	0·29	4·1

There can be no doubt in the light of these experiments that the greater gain in weight is due to the more rapid entry of solution into the cells.

In an experiment with pieces of *Laminaria* stipe, in which imbibition plays a predominant part, no such rapid absorption of water was observed, solutions entering on the contrary in all cases more slowly than water.

Osmic acid. Of the other poisons with which experiments were made the only one which produced a similar acceleration of the rate of entry of water was osmic acid (Fig. 4) and the effect was only observed in the much lower concentration of M/1000. On the other hand the subsequent loss of weight was very slow and in
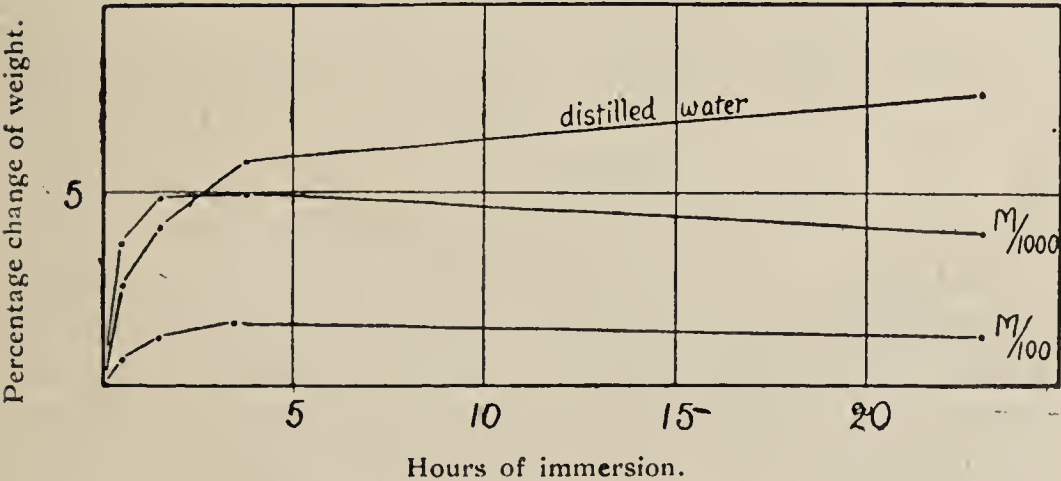
FIG. 4. Osmic acid.

marked contrast with the rapid fall of the curves for all strengths of mercuric chloride.

Mercuric cyanide. The toxic effect of mercuric cyanide in similar concentrations was at first simply evidenced (Fig. 5) by depression of the rate of entry of water below that in equi-molecular sucrose solutions. Eventually, however, a fall in weight ensued, which was less rapid and set in much later than with mercuric chloride, but was more pronounced than with osmic acid.
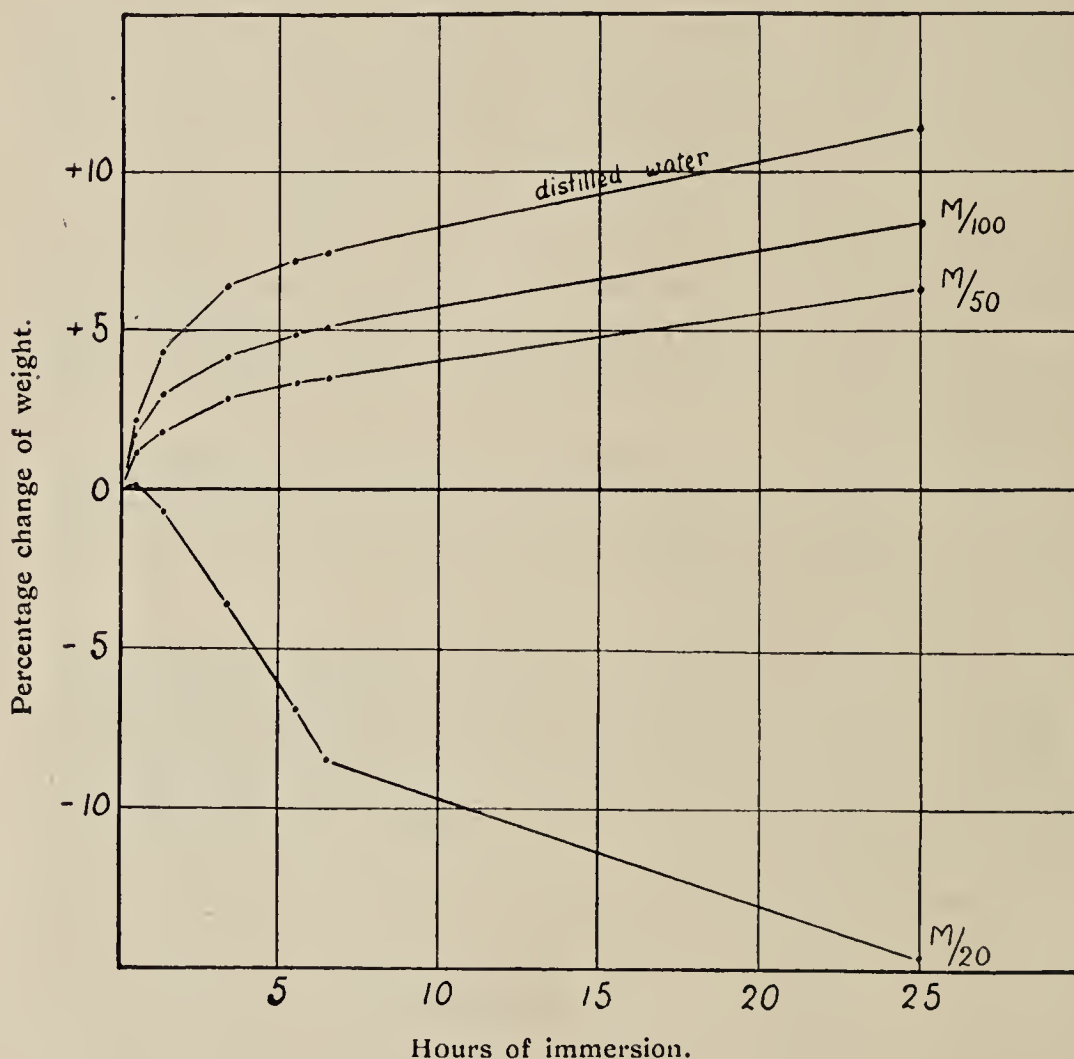
Fig. 5. Mercuric cyanide.

Chloroform. The effect of the M/20 solution of chloroform (Fig. 6) illustrates in a striking way the powerful effect of chloroform in increasing the permeability of protoplasm to solutes. The curves for the weaker solutions are similar to that for distilled water, but at lower levels—a type of curve apparently distinct from those already figured.

Fig. 6. Chloroform.

REMARKS ON THE RESULTS OBTAINED WITH SOLUTIONS
OF TOXIC SUBSTANCES.

It would serve no useful purpose to attempt at this stage any detailed discussion of the results; but some remarks and tentative suggestions seem to be warranted.

Fig. 7. · Comparison of the effects of different substances.

To facilitate a comparison of the different types of curve and
as a convenient summary of the main results, Figs. 7 and 8 have
been drawn. The curves are smoothed out approximately from the
curves obtained in different experiments, but are not intended to be
quantitatively exact or accurately comparable.

The powerful effect of the anæsthetic and lipoid solvent,
chloroform, has already been referred to, and the marked increase
of permeability caused by it affords a sufficient explanation of the
rapid escape of water (accompanying the exosmosis of sap solutes)
in an M/10 solution. The interpretation of the curves for the still
more dilute solutions must remain for the present uncertain.
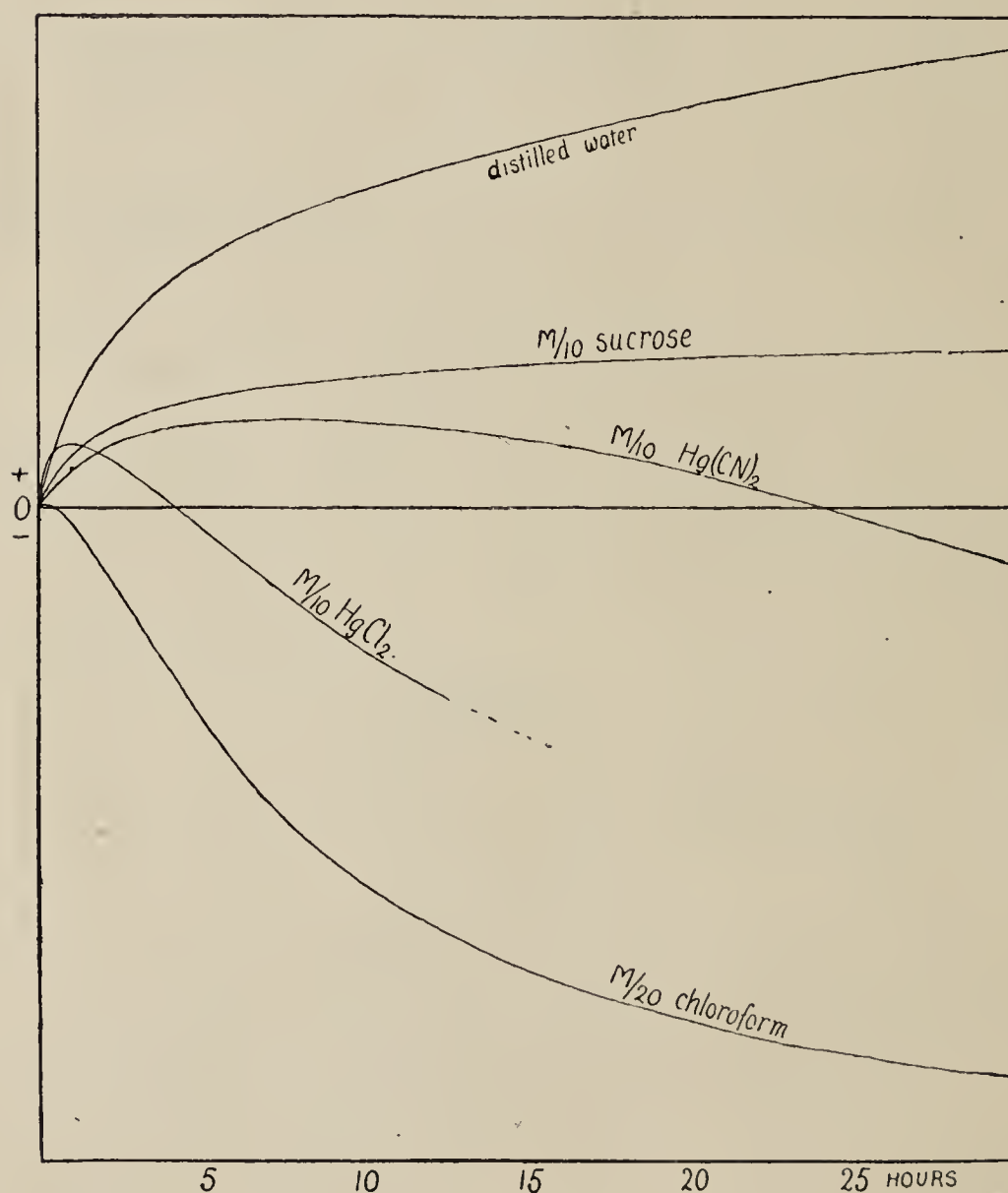
FIG. 8. Comparison of the effects of different substances.

According to Osterhout,[1] very dilute solutions produce a reversible decrease of permeability to electrolytes in the thallus of *Laminaria ;* and this would probably be correlated with increased resistance to the osmosis of water. If the same hold for protoplasm generally such a dilute solution should give a curve lower than that for an equi-molecular solution of an inactive substance, such as sucrose appears to be, but of similar form ; except that the final total expansion might be somewhat greater owing to the protoplasm being rendered a more nearly perfect semipermeable membrane.[2]

The M/100 solution (0·12%), the weakest used, should, however, on the basis of Osterhout's results give a different type of curve, causing first a reversible decrease, later an irreversible increase of permeability ; but there is no sign even in the curve for the M/50 solution of the exosmosis which would follow in this later stage. A repetition is desirable with larger volumes of solution and every precaution against dilution during the course of a prolonged experiment. Solutions rather stronger, which produce at once (as far as Osterhout could observe) an increase of permeability, should give a curve showing at first a diminished rate of entry of water, due however to exosmosis of solutes, not to decreased permeability to water—the same form of curve, in fact, as is obtained with mercuric cyanide.

With the latter, the results are explicable on the basis of an increase of permeability and consequent exosmosis of solutes which vary in degree and rate with the strength of the solution. The more rapid fall after the first five hours in the M/100 and M/50 than in the M/10 may be due to the larger volume of solution that had entered and therefore a probably deeper penetration. The M/100 solution of mercuric chloride contrasts similarly with the other strengths of that salt and the same explanation may hold.

Mercuric chloride precipitates the proteins of the membrane, and quickly makes exosmosis possible, though this is far less rapid than with chloroform, perhaps partly because of a more general permeation of the tissue by the latter.[3] Although chloroform is very soluble in lipoids, it would be less firmly held than is mercuric

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[1] Science, 37, 1913, p. 111.

[2] On the effect of permeability on the isotonic coefficient and the maximum degree of turgor, compare Lepeschkin, 1909, Ber. d. d. Bot. Ges. XXVI a, p. 198, and XXVII, p. 129.

[3] Chloroform vapour may diffuse to the interior by way of the air spaces.

chloride, which accumulates first in the peripheral cells[1] and only gradually penetrates to deeper layers. On the other hand, the more rapid entry of the M/100 solution than of distilled water suggests that the precipitation of proteins results first in a lowering of the resistance to the entry of water without making exosmosis of solutes possible, or at least a sufficiently rapid exosmosis to produce a counterbalancing reduction in the force under which water enters.

A similar explanation would hold for M/1000 osmic acid.[2] The curves for this powerful fixative indicate a relatively small increase of permeability, and there is little or no evidence of this increase continuing progressively; but again further experiments are clearly required.

Experiments were made with other substances, in addition to those already mentioned, but only a brief indication of the general nature of the results is warranted. The curves for solutions of copper sulphate were very similar to those for equi-molecular solutions of mercuric cyanide. Thus, with potato, the membranes do not oppose the passage of the former, like the coat of the barley grain, which differentiates sharply between it and the scarcely ionised mercuric cyanide.[3]

Phenol in concentrations of M/100 and M/1000 gave curves only differing from the curve for distilled water within the limits of experimental error; similarly M/1000 picric acid. Picric acid in M/100 concentration quickly started exosmosis, but the rate of fall in weight was as slow as with osmic acid. Alcohol in M/10 solution gave a curve which was nearer to that for distilled water even than M/25 sucrose, showing that it entered the cells readily, but without injuring the membrane appreciably in its relation to the sap solutes.

Discussion of the general question of the osmotic relations between a tissue and solutions is reserved for a subsequent paper.

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February, 1918.

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[1] See p. 61.

[2] Comparison with the more rapid swelling of proteins in acid solutions than in water does not appear to the writer helpful when the quantity of protein in the material is so small. Cf. Stiles and Jörgensen, V, *loc. cit.*, p. 429 and 432.

[3] Adrian J. Brown, *loc. cit.*, 1909, p. 88, etc.

THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.

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Chapter V.

THE PAPPUS.

THE matter in the previous chapters has not been controversial to any marked extent. Any controversies which there have been, such as those on the venation of the corolla and on the function of the hairs on the styles, are now dead, but the question of the phyllome or trichome nature of the pappus is still in dispute. The evidence which has been previously adduced is therefore given in some detail in Section A and additional facts which help to present the matter in a new light, are brought forward in Section B. The whole of the fruit might have been considered in this chapter but as the structure of the fruit, apart from the achenial hairs and the pappus, seems to have little or no phyletic[1] value, (cp. Lavialle, Chap. I, Sect. B), it is omitted from the present discussion. As the question of the use of the pappus in fruit dispersal seems closely allied to the subject of geographical distribution it, also, is omitted and will be considered in a later chapter.

A. History.

Morison (52) was one of the first to use the presence or absence of the pappus as a character for the sub-division of the family ; Ray (57) and others followed. Vaillantus (67) distinguished three types, pilose, plumose and coroniform. The aculeate or aristate type was added by Boerhaave (7) and the squamose or paleaceous type by Pontedera (55), who also distinguished the " corticose " fruit of *Calendula* and the " osseous " fruit of *Osteospermum*. Forty years later Berkhey (6) gave some figures of the various types and enumerated the coroniform, pilose, plumose, sessile and stipitate types. Gaertner (20) in his special study of fruits made some advance, distinguishing foliose, capillary, setose, plumose, spiny, penicillate and aristate forms.

The details of the various types of pappus, like most other floral details in the Compositæ, were most fully developed by Cassini (11, 4th Mem.). Thereafter these data were applied in all taxonomic systems.

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[1] The biological or economic value may, of course, be considerable, *e.g.* the mucilaginous pericarp in many species (14), and the use of sunflower fruits as a source of edible fats.

The Cichorieæ being such a uniform group, the pappus here has received special attention. Cassini (11, Tome I, p. 380) used the pappus with other characters of the fruit, and Don (15) also used the pappus with other characters in his classification of the Cichorieæ. De Candolle and Bentham followed Cassini; Hoffman (34) suggested a very simple but very artificial classification on the coroniform, plumose or pilose pappus but this was rejected as already mentioned (Chap. I, Sect. A) by Engler and Gilg (18).

Taxonomic Value of the Pappus.

The above is one example of the use of the pappus in taxonomy. As usual the use of only one character gives a very convenient but unnatural grouping. Another example is the importance attributed to this part of the fruit by Hutchinson (37 and 39) and his use of the presence or absence of the pappus in the separation of *Brachymeris* and *Marasmodes* (37). This author considers the pappus "one of the most important features in the consideration of the phylogeny and affinities of the genera of this interesting family." In accordance with this view he takes the absence of the pappus with the absence of glandular pits from the leaves as forming a difference of generic value (*loc. cit.*).

In contradistinction to the views of Hoffman and Hutchinson we have Bentham (5, p. 354) on the pappus as follows: " it is on the ripe achene that it has attained its fullest development in those innumerable variations which strike the eye of the most superficial observer, and which have been eagerly seized upon to characterize a large proportion of the thousand and one petty genera with which syantherology has been encumbered. Constant or nearly so in each species, with very few exceptions, the pappus will often, in a most natural genus, so vary from species to species as to make it a most difficult task to decide whether it should be neglected altogether, or, if taken into account, what modifications may be taken as generic, sub-tribual, or tribual. The presence or absence of a pappus or its degree of development is always of much less importance than its nature when present." As a result of the analysis of the pappus forms given below the writer is of a similar opinion.

The new genera, *Triplotaxis*, Hutchinson (36) and *Cavea*, Smith and Small (62) are examples of the value of the structure of the pappus when present, but the case of *Bidens* and *Coreopsis* makes an interesting commentary. *Bidens* is characterized by downwardly projecting barbs on the aristæ of the pappus; *Coreopsis* is distinguished from *Bidens* merely by the upwardly projecting

barbs, but *Coreopsis aristosa*, Mich. is described (23) as having no pappus at all or aristæ with downwardly or upwardly directed bristles. These forms abound in the same locality and the probability of hybridisation is negatived by the absence of *Bidens* from the districts where these forms occur.

Dispersal Mechanisms.

Hildebrand (30) considers the pappus at some length in its relation to dispersal by wind and by animals. In his general memoir (32) also he gives figures and details of a number of hooked and pappose fruits in the Compositæ having previously developed the subject of dispersal by hooks in a special contribution (31). Hooked fruits in the Compositæ are also considered by Huth (41). Yapp (71) and others have described various Composite fruits in which the pappus is glandular and sticky.

The presence of a pulvinus at the base of the pappus either in the form of a ring or isolated at the base of each seta has been noted by Schenk (59), Taliew (65), Haberlandt (22), Hirsch (33), Steinbrinck (64) and Yapp (71).

Taliew distinguishes three types of mechanism for the spreading of the pappus in dry conditions, I—the *Lactuca* type with an annular pulvinus, II—the *Tussilago* type with no pulvinus but unequal thickening of the pappus hairs, III—the *Cirsium* type with a pulvinus to each seta. The first type was recorded by Schenk and Taliew in all the Cichorieæ and most of the Tubulifloræ examined. The second type in which each seta curves on drying occurs chiefly in the Tussilagininæ. The third type is characteristic of the Cynareæ, and experiments by the writer show that in the case of *Centaurea imperialis* the mechanism is very sensitive to the degree of the humidity of the atmosphere. With a Relative Humidity of ·78 the pappus remains closed, or, if opened by drying in a warm test-tube, closes rapidly when brought into the air. With the R. H. ·77 it remains open for some time after previous drying and with the R. H. ·75 it opens spontaneously and remains spread at an angle of 45" for an indefinite period.

There are various other contributions to this part of the subject but they are concerned more directly with fruit dispersal and will be dealt with in a later chapter.

Pericarp Structures.

Capus (10), Hanausek (24-25), Portheim (56), Lavialle (45) and Loose (46) have recorded the detailed structure of the pericarp in

many genera. The phylogenetic results obtained by Lavialle have been mentioned already (Chap. I, Sect. A, and Fig. 3). In addition he gives a very complete summary of our knowledge of the fruit in the Compositæ, dealing with the ovule, epithelium of the embryo sac, the haustorial function of the antipodal cells and other matters, which may have a certain phyletic value but which are outside the scope of the present chapter.

Joxe (42) gives details of the various types of germination in the Compositæ, some of which are quite aberrant. Hanstein (27), Haberlandt (22) and Yapp (71) mention the capitate hairs which are so characteristic of certain genera, notably *Helianthus*, *Calendula* and *Inula*.

Achenial Hairs.—The most interesting part of the pericarp from the present point of view is, however, the hairs which occur on very many of the fruits. These were studied in detail by Macloskie (49), and, as they appear to be of considerable phyletic value, they will now be considered in some detail. The curious duplex hairs of the cypsela of *Senecio vulgaris* have long been objects of interest. They are situated in the furrows between the ridges of the pericarp, and are composed of two cells placed side by side, each containing a spiral fibre, which on being moistened swells and shoots out at the top of the cell, showing movements like those of the elaters of the liverworts. This double tube is mounted on a pedestal of two clear cells (Fig. 11).

Archer (1) and Kraus (44) mention these duplex hairs as common in the Compositæ. Macloskie examined genera from most of the tribes, and says " the consideration of the facts stated above suggests a somewhat different line of affinities from that usually adopted." He did not, however, make any definite phyletic suggestion. Harz (28), Heineck (29), Nichols (53) and Lavialle (45) extended the observations, but again drew no definite phyletic con- clusions, so that we are free to make what use we can of the facts.

The duplex hairs with elaters are characteristic of the Senecioneæ, similar duplex hairs with acute tips and no elaters, occur in the Astereæ, Eupatorieæ, Vernonieæ, Heliantheæ, Helenieæ and Arctotideæ. The Anthemideæ have no such hairs but cells with spiral filaments occur on the outside of the pericarp in certain cases (Figs. 12-13).

The Calenduleæ are probably similar to the Senecioneæ according to Macloskie, with the addition of the above-mentioned capitate hairs. The cypsela of the Cichorieæ is glabrous but

shows denticulate epidermal cells, and below these in many cases cells with spiral filaments (Fig. 14).
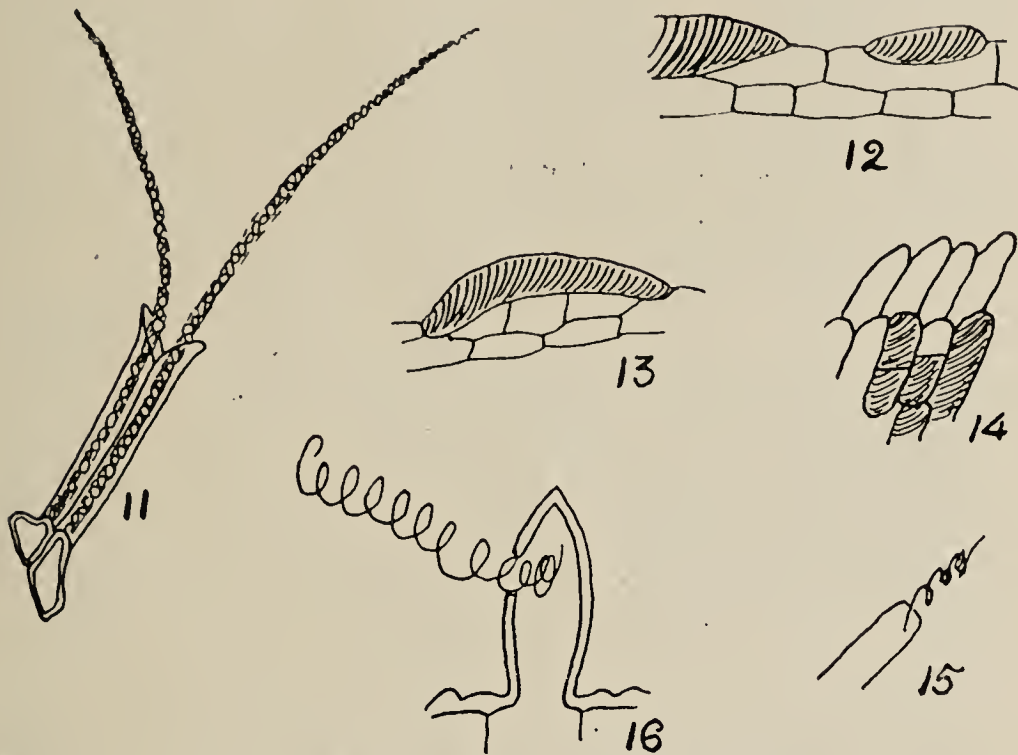
ACHENIAL HAIRS OF COMPOSITÆ.

FIG. 11. Duplex hair of *Senecio vulgaris*; Fig. 12. Elater cells of *Chrysanthemum Leucanthemum*; Fig. 13. Ditto of *Maruta Cotula*; Fig. 14. Endocarpal filaments and denticulate epidermal cells of *Lactuca scariola*; Fig. 15. Endocarpal fibril of *Cirsium lanceolatum*; Fig. 16. Elater cell of *Trixis*. Figs. 12-15. after Macloskie, Fig. 16 after Lavialle.

The Cynareæ vary; some have duplex hairs as in the Astereæ, others have simple hairs, and others again show endocarpal filaments as in the Cichorieæ (Fig. 15). *Centaurea* shows simple hairs. The Inuleæ have duplex hairs similar to those of the Astereæ but with obtuse tips. In view of the suggestion that *Cavea* (Plucheinæ) is an intermediate type between the Inuleæ and Cynareæ (see Chap. IV) it is interesting to note that the typical Asteroid hairs occur in *Pluchea foetida* (Plucheinæ) as well as in the Cynareae.

One of the most interesting points is the variation in the genus *Trixis* of the Nassauviinæ. According to Lavialle (op. cit.) *Trixis Lessingii*, *T. verbasciformis* and *T. mollissima* have one or two-celled simple hairs, but *T. pallida*, *T. Hieronymi*, *T. ochroleuca* and *T. brasiliensis* have simple hairs with spiral elaters (Fig. 16). If this is read in connection with the suggestion of *Trixis* as the primitive genus in the Nassauviinæ (see below, Sect. C.) the phyletic value of these hairs becomes obvious.

If the *Senecio* type of duplex hair be taken as primitive, it is clear that it has passed through several forms of reduction along the various lines of evolution suggested in Fig. 7, Chap. II, the elaters disappearing more or less in the Inuloid, Helianthoid and Asteroid lines, the hairs becoming reduced to single elater cells in the Mutisieæ or to short external cells in the Anthemideæ and, perhaps, passing below the epidermis in the Cichorieæ. It is doubtful, however, whether the endocarpal filaments in the Cichorieæ and Cynareæ are homologous with the elaters.

Development.—Before Buchenau published the first complete account of the development of the floret in 1854 (8a), Duchartre (16) had recorded some observations on *Helianthus*, from which he concluded that the two paleæ on the top of the cypsela were epicalyx leaves or bracteoles, fused with the ovary for part of their length ; the calyx he considered to be completely fused with the lower part of the corolla tube. Duchartre also regarded the pappus in *Bidens* and all paleaceous pappi to be of a similar epicalycine nature.

In subsequent observations apart from the phyllome or tri-chome nature of the pappus, the chief point recorded is the origin of that structure after the corolla and stamens have been dif-ferentiated, see Chap. IV, Sect. A, and the literature there cited.

An isolated but interesting observation is that by Baart de la Faille (2), who, as an example of his thesis that logarithmic distribution is more frequent in nature than the normal curve, takes the top cells of the pappus in *Senecio vulgaris,* and shows that any increase in length is directly proportional to the length already acquired.

Phyllome v. Trichome.—The question of whether the pappus in the Compositæ is a modified calyx-limb or merely hairs or emergences on the top of the so-called calyx tube is still a question of controversy, the latest contributions dating from 1916.

The controversy reached its height about 1873, but Richard (58) had previously stated that the pappus had been recognised for a long time as analogous to the calyx of other families. He adds as a caution "néanmoins ce seroit une grande erreur d'assimiler en tous points l'aigrette aux calices ordinaires." Cassini (11, Tome I, p. 202) describes the pappus as "un calice épigyne, d'une nature particulière" and analogises it (op. cit., p. 219) with the paleæ of the receptacle and with the involucral bracts. His argument is "ces paillettes et ces écailles sont incontestablement des bractées.

Donc l'aigrette est un assemblage de bractées, lesquelles sont disposées à peu près celles des calices ordinaires ; donc l'aigrette est un calice." This is typical of much of the loose and superficial reasoning on the subject. On p. 273 (op. cit.) he evidently takes the squamellules of the Cynareæ as bracts, cp. below, Sects. B-C.

Kohne (43) supported the phyllome theory on account of the insertion of the setæ in several genera at five points, after the manner of the pentadelphous stamens in *Hypericum.* The setæ were, therefore, regarded as divided calyx leaves, while Cassini and others regarded them as single sepals and the calyx as having undergone *dédoublement.*

Buchenau (8b) is quoted by Masters (51) for the trichome theory and by Lund (47) for the phyllome theory. This is because he at first supported the former theory and then partially withdrew in the paper quoted. He definitely states that there is a calyx, and then goes on to show that the pappus hairs and scales are accessory organs of the semi-aborted calyx and not organs of the same importance as the other appendicular organs of the flower. He quotes cases where a pappus was observed inserted on five or more green leaflets which were provided with vascular bundles and developed in inverse proportion to the pappus.

Lund (47) maintains that the pappus must be of a phyllome nature, each seta being a sepal, because in *Cirsium* and other genera vascular bundles of a more or less rudimentary nature are present in the paleaceous setæ. According to Lund (op. cit., p. 259) " l'aigrette des Composées est un véritable calice." This same opinion is expressed by Treub (66) as a result of finding all stages in the passage from the normal pappus to five free leaves with vascular bundles in the galls which sometimes occur on the capitula of *Hieracium umbellatum.*

Bentham (5, pp. 354-5) repeatedly mentions the fact that the pappus is generally regarded as a reduced or modified calxy-limb, but he remained non-committal on account of the many variations with which he was familiar. He says " their homology is not so easy to settle," and again, " the occasionally present, reduced, innermost row . . . may only be a modification of the epigynous disc."

Eichler (17) gives a full account of the controversy to his date 1875, quoting Hofmeister (35) and others as regarding the pappus as an isomerous, oligomerous or pleiomerous true calyx, and further authorities for the trichome or emergence nature of the organ.

Eichler considered both these views wrong and regards the pappus as a modified calyx. He quotes the cases with a reduced number of paleaceous setæ as proving the leaf-nature of the pappus (cp. below, Sect. B).

Coulter (12) and Martin (50) consider the pappus as a calyx, the liberation of the upper part being retarded in the development of the flower. Worsdell takes a new line of argument (69, p. 954), " if the pappus is not the homologue of the calyx, where are we to look for the latter in the normal floret ? for it cannot be supposed to be entirely absent." Baillon (3) had previously stated that in the case of *Xanthium* there is nothing in the flower at any age which represents a true calyx. Worsdell (70, p. 77) considers that a pappus may also arise from supernumerary petals, as in the *Leontopodium alpinum β nivale* observed by De Candolle (9), and also states (70, p. 66) that " normal examples of the multiplication of sepals are seen in the pappus of the Compositæ." Hutchinson (39) follows Worsdell.

Warming (68) pointed out that the pappus hairs could not be sepals because they do not occur in the position of sepals, and because they have a function usually attributed to hairs. He regarded the pappus hairs as " epiblastemes " which differ essentially from the more highly organised " epiblastemes " and considered that the true calyx of the Compositæ is the slightly developed annular ridge at the top of the cypsela from which the pappus hairs arise. The rudimentary vascular bundles on which Lund laid so much stress are considered by Warming to be of little importance.

A similar view was held by Hänlein (26) and Masters (51). The latter answers the teratological arguments of Treub and Worsdell, when he points out that " the occasional development of an organ which is usually suppressed does not prove that the parts that are generally present, like the pappus, are necessarily modified representatives of abortive organs." Taliew (65) states as an accepted fact that the setæ have the character of emergences in all the types examined by him. McNab (48) in reviewing Lund's work considers that, although in some cases the pappus scales may be sepals, " in the majority the scales or bristles or hairs of the pappus are undoubted trichome structures."

Such is the controversy in which the two chief British teratologists disagree in the most decided way, in which more or less detailed observations of a limited number of species are used to support the phyllome theory, while the general and well-known facts

of structure and position are used to support the trichome theory. The view adopted in most text-books is that of Richard and Eichler that the pappus is a modified calyx limb, but it seems to the writer that Goebel's argument (21, p, 317) concerning the nature of the receptacular setæ is quite applicable in this case also. It runs as follows—"Where now instead of single parts of a hypsophyll we see 'bristle-scales,' a qualitative change has taken place which may have begun with a transformation of the single parts of the hypsophyll, but I see no ground even then, if the hypsophyll no longer exists, for keeping its ghost hovering above, or rather below, these bristle-scales; to assume that it still exists is an 'idea,' and this 'idea' is stuck somewhere in the axis and allows only the bristle-scales to appear. Such 'ideas,' however, are to be found even in recent botanical literature."

This may be applied with more appropriateness on account of the evidence given below for the primitiveness.of the setose pappus within the family and the compound setose character of even the reduced number of paleaceous structures so frequently quoted as being very similar to a true calyx.

B. Structure of the Pappus.

When we examine the actual structure of the various types of pappus most of the difficulties connected with the trichome and phyllome theories disappear. We must, however, be content to regard the pappus as a structure more or less *sui generis* as advised by Richard.

As with the styles and stamens we can reduce the innumerable variations to a limited number of mean types which pass gradually into one another. These mean types will now be described briefly. The fundamental type is the scabrid seta, composed of uniseriate rows of cells fused together, with the obtuse terminal cell of each row free and projecting outwards as a lateral cilium for a distance which is less than the diameter of the seta. This is described as *setose scabrid* or *setose denticulate* (Fig. 17, A). That the structure is a fusion of uniseriate hairs such as are common on the cypsela is obvious and really requires no comment.

There are various modifications of this basal type; if the ends of the constituent hairs do not project the seta is simple, as in *Tussilago*, and the upper part may be unicellular in cross-section as previously mentioned (61). This is described as *simple setose*, (Fig. 17,B). The projecting lateral cilia may be acute and arranged in a

serrate fashion, then the pappus is described as *setose serrulate,* (Fig. 17, C). If the lateral cilia are as long as or slightly longer than the diameter of the seta, the pappus is described as *setose barbellate,*(Fig. 17, D). This form leads on by the elongation of the lateral cilia to the *setose plumose* type, (Fig. 17, E), where the projections are considerably longer than the diameter of the seta.

Setæ of these various types occur in large numbers, in one or two or more rings on the top of the cypsela, and there is no commoner modification than the fusion of the setæ at the base, to form a more or less continuous membranous collar of tissue. This modification is quite in harmony with the tendency to reduction and cohesion present in other floral members. It is duly noted by Hoffman (34) in his non-committal description of the various modifications of the pappus. It is included in many descriptions of species, such as *Vernonia Kerrii* (13), and is frequently a character of generic rank. It occurs in the sub-genus of *Senecio, Senecillis* (19). It was noted in *Tussilago* by the writer(61) and occurs in a very large number of genera.

This being the case it is not surprising to find that sometimes the collar is discontinuous and broken up to give a number of scales, paleæ or squamellæ. The setæ frequently vary in length, so that fusion gives a form described as *paleaceo-setose* (Fig. 17, F). The paleaceous part may be comparatively short or relatively long on the same fruit. The addition of one or more setæ to the central rib or the further thickening of the single central seta gives a similar type, which is usually ciliate at the edges, as in *Gaillardia,* and is known as *aristato-paleaceous,* (Fig. 17, G). By a slight elongation and a crowding together of the lateral cilia, as in *Centaurea calocephala* (22, Fig. 220. p. 545), we get a *serrulato-paleaceous* form (Fig. 17, H). If the constituent setae are of equal length and fuse completely a *simple paleaceous* type (Fig. 17, I) results.

It may be rather surprising that this simple fact of the trichome nature of the paleæ has not been more widely recognised. Anyone can mount the simple paleæ of *Berkheya* or *Tagetes* and see with oblique illumination under the low power of a compound microscope that the facts are as stated. The free ends of the constituent hairs can be seen distinctly and the ribbed surface is obviously formed by the fusion of the constituent setæ.

If the ends of the setæ are free to a slight degree the result is a lacerate margin, giving the *fimbriato-paleaceous* type, (Fig. 17, L).

The plumose seta by the fusion of the lateral cilia in the same way as in the *serrulato-paleaceous* type gives rise to the *plumoso-paleaceous*
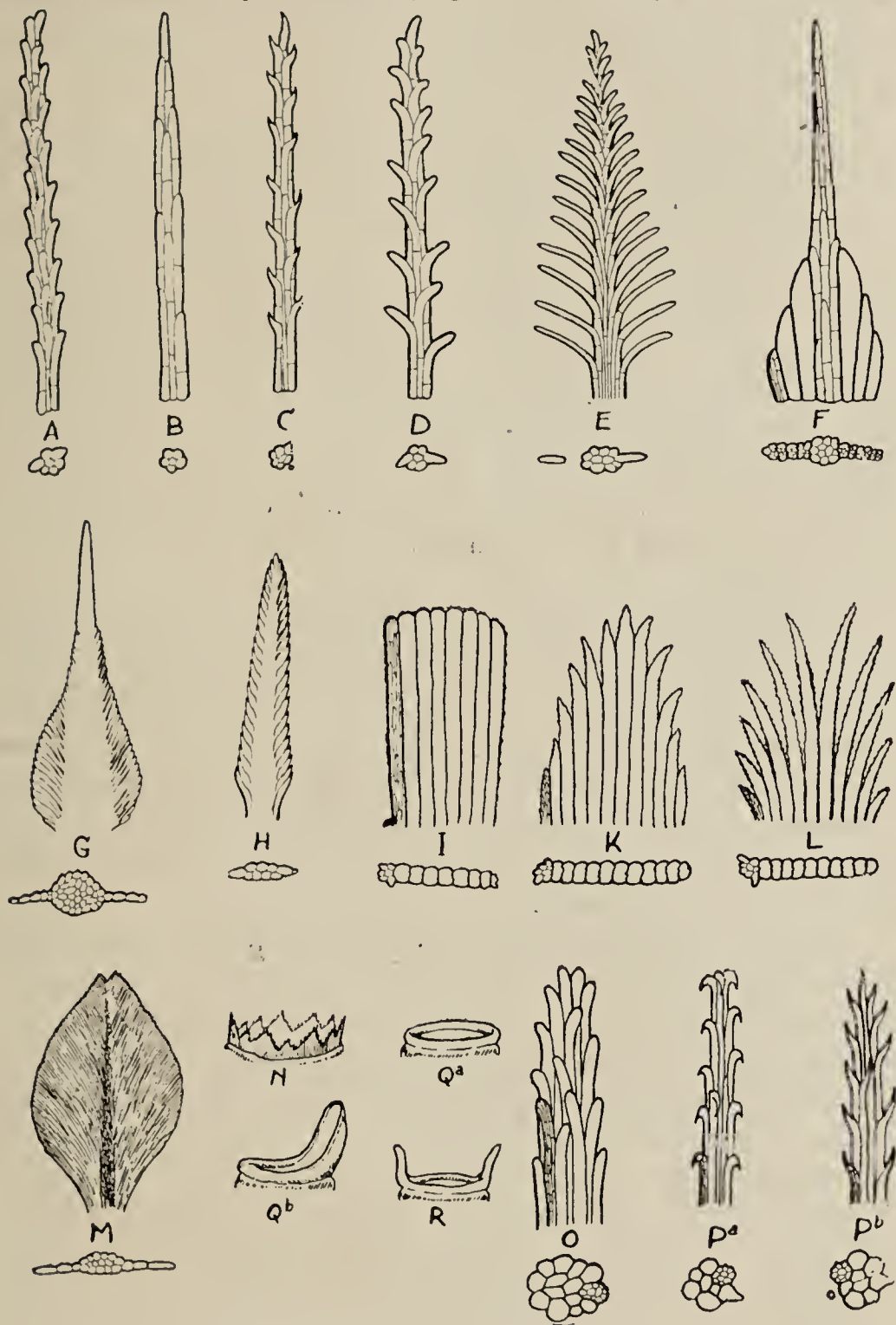
PAPPUS-FORMS IN THE COMPOSITÆ.

FIG. 17. Below each figure of the surface view a tranverse section is given in most cases. The individual setæ are outlined by heavy lines ; the constituent hairs are indicated by thin lines, in some cases only in part for clearness. – A. setose scabrid ; B. simple setose ; C. serrulato-setose ; D. barbellato-setose ; E. plumoso-setose ; F. paleaceo-setose ; G. aristato-paleaceous ; H. serrulato-paleaceous ; I. simple paleaceous ; K. fimbriato-paleaceous ; L. setoso-paleaceous ; M. plumoso-paleaceous ; N. fimbriato-coroniform ; O. aristate ; Pa.Pb. barbato-aristate ; Qa. coroniform ; Qb. auriculato-coroniform ; R. aristato coroniform.

type, (Fig. 17, M), with a structure very closely resembling that of a feather. This occurs notably in *Ursinia*; the paleæ here make very pretty objects under oblique illumination and the structure is quite apparent even to the uninitiated.

As mentioned above, the setæ are frequently more or less connate at the base, and by the abortion of the free parts we get another common form, the *fimbriato-coroniform* type (Fig. 17, N).

In these paleaceous forms the setæ are fused laterally with one another, but they may also fuse in a clump, when a thick, more or less rigid structure arises, which is known as *aristate* (Fig. 17, O). The free ends of the setæ are usually blunt and project to a slight extent, but each seta may end in a large, strong, acute bristle. This type is described as *barbato-aristate*, and the bristles may project downwards, as in *Bidens* (Fig. 17, P^a), or upwards, as in *Coreopsis* (Fig. 17, P^b). These aristæ are frequently few in number, as one would expect when it is remembered that a number of setæ go to form each one.

Just as the paleaceous types by extreme reduction give type N, these aristate types by fusion and reduction may give a thick, cartilaginous ring at the top of the cypsela, which is described as *corneo-coroniform* (Fig. 17, Q^a). This ring may grow out on one side to form an ear-shaped or *auriculato-coroniform* pappus, (Fig. 17, Q^b). The auricle may be simple or lacerate like type K, *e.g.*, *Pentzia* (see 38, Plate X). Finally by a similar reduction we may get two horn-like projections (Fig. 17, R).

Evolution of the Pappus-forms. Most of the evolution of the various types of pappus is obvious, but a diagram (Fig. 18) is given for convenience. The setose-scabrid type is taken as primitive and by fusion at the base with subsequent reduction gives type N. This *fimbriato-coroniform* type, like the simple paleaceous type, I, is clearly polyphyletic and may be derived easily from a number of types such as B, F, L and K. The evolution of the *serrulato-paleaceous* type, H, is clearly through type C. The various steps towards, or the direct evolution of types F, I and M are indicated, and the various types arising from the aristate type, O, are arranged so that downward lines are lines of reduction and upward lines are lines of progressive differentiation.

The inter-relationships and possible evolutionary connections of the various types are somewhat more complex than in Fig. 18, but it is considered unnecessary to complicate the matter further since alternative methods of evolution of such types as F, G and M,

will be obvious to the reader. The main point is that the setose type is primitive and the paleaceous, coroniform and aristate types derived.
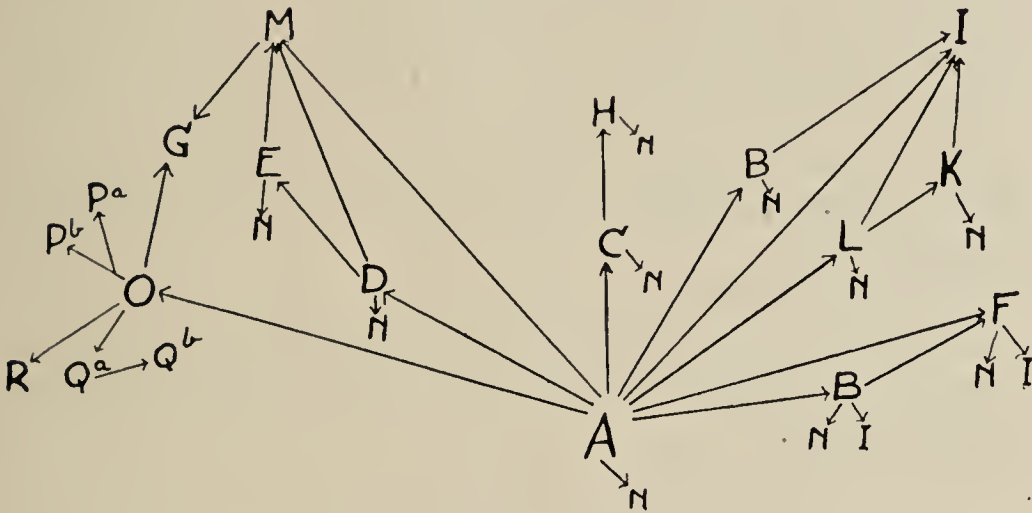
· FIG. 18. Evolution of the Pappus-forms in the Compositæ.

The origin of the plumoso-setose type from the barbellato-setose type has been previously noted by the writer (62). The origin of type N from type K is a very obvious explanation of the well developed fimbriato-paleaceous pappus described by Békétoff (4) in an anomalous *Cichorium Intybus*. The origin of type N from type F explains the frequent mixture of short lacerate squamellæ with a few awn-like, elongated squamellæ, as in *Helianthus scabra* (54). Similarly the origin of the aristæ, by the fusion of setæ explains the frequent variation in the number of aristæ, even in a genus such as *Bidens*, where they are an important diagnostic character, but in which the aristæ vary from two to ten (60).

It is clear from the above details that the primitive pappus in the Compositæ has a trichome structure, whatever its homologies may be, and that the foliose calyx limb, when it occurs teratologically must be regarded as a reversion to a pre-Composite ancestor. It will be shown in a later chapter that there is every reason to believe that the Compositæ were derived from genera such as *Siphocampylus* in the Lobelioideæ, in which the calyx limb is frequently very much reduced or even (as in *S. eximius*) altogether absent.

Where a calyx limb is present in addition to numerous hairs of various kinds showing similar modifications to those of the pappus, as in *Triumfetta* (93, and see also 32), there has as yet been no suggestion of homologising the hairs of the fruit with the calyx limb. Masters' argument that the absence of one set of organs is no proof

of the nature of another set which is present, seems to the writer very appropriate.

The five-point insertion of the setæ and the frequency with which five or ten occurs as the number of paleæ or aristæ is quite explicable by the simple physiological fact that the food supply is naturally greatest near the five or ten vascular bundles which supply the ovary wall in most genera. As these bundles also supply the margins of the petals it follows that the paleæ and aristæ, when five, alternate with the petals and thus develop in the position of sepals.

Thus the application of a little microscopy combined with an obvious application of elementary physiological facts removes the clouds of controversy and lays "the ghost of the hypsophyll" which troubled Goebel.

C. Analysis of the Pappus-Forms.

Having determined the structure and evolution of the various mean types of pappus we can now analyse the distribution of these types throughout the family, taking the tribes in the order which is suggested by other phyletic data. As the pappus shows great variety, sometimes even in the same genus, it will be necessary to consider the tribes in some detail.

Senecioneæ. In the basal genus, *Senecio*, the pappus is usually copious and setose scabrid, but it varies to simple setose and is sometimes barbellato-setose, or of fewer, thicker, almost aristate setæ, which may be paleaceous at the base, as in § *Senecillis* (=*Ligularia glauca*, Hoffm.), or the scabrid setose type may be paleaceous at the base, as in *S. Grahami*, Hook. It may also be reduced to very short setæ or may be altogether absent.

The closely related genera, *Culcitium*, *Gynura*, *Cineraria*, *Emilia* and *Gynoxys* are all setose scabrid or barbellato-setose with the setæ in one, two or more rows as in *Senecio*. The genus *Raillardia*, which Hoffman removes to the Heliantheæ, and *Raillardella* are plumoso-setose. The other genera are all setose scabrid.

In the Tussilagininæ the simple setose type occurs in *Tussilago*, but the other genera are setose scabrid or barbellate. All the Othonninæ and most of the Liabinæ are similar but in some species of *Liabum* an outer row of short, fimbriato-paleaceous scales occurs. In the Senecioneæ, therefore, all the primitive types, A, B, D, E,

L, K, and O, occur (cp. Fig. 18). Of these primitive types the lower forms, A, B, D and O, occur in *Senecio.*

Cichorieæ. The pappus here may be absent or reduced to the fimbriato-coroniform type ; usually, however, there are one, two or more rows of scabrid setæ. In *Tragopogon* and its allies the setæ are usually plumose, frequently very elaborately so, with the primary and secondary cilia forming a network. The setæ are frequently connate at the base and deciduous, either singly or in a ring if connate.

In *Cichorium* there are two or three rows of short, connate paleæ, giving type N, but in allied *genera* the paleæ are fewer, longer and fimbriato-paleaceous, sometimes prolonged into awns as in type G, sometimes, as in *Hymenonema*, there are numerous barbellate setæ in the external rows and fewer sub-paleaceous setæ in the inner rows. This duplex or triplex pappus, apparently foliose in one row and setose in others, is very difficult to explain by the phyllome theory but has a quite simple and obvious explanation if the fusion of setæ is a "critical tendency," as advocated in Section B. A transition to the corneo-coroniform type occurs in *Koelpinia*, where the aristæ are short and connate at the base.

Calenduleæ. Setæ are rare in this tribe ; *Dipterocome* has five to ten setæ with the addition of two appendages of type R and a few species of *Osteospermum* have one row of scabrid setæ. In the other genera the pappus is either absent or of types N or Qb.

Arctotideæ. According to the previous data *Ursinia* is probably the basal genus here. The pappus of that genus is composed of five paleæ of type M. The compound setose character is obvious as mentioned above and it will be noted that type E occurs in the Senecioninæ. In addition, however, a few setiform paleæ of type F or G are sometimes present as an inner row, so that we have the complete series of allied forms in this genus and the sub-tribe from which it is suggested to have arisen. In the other genera of the Arctotidinæ the paleæ are usally numerous, types I or K; type F occurs in *Haplocarpha*, a modified combination of types N and Qa in *Cryptostemma* and numerous paleæ of type I in *Arctotis*. The pappus is absent in a few genera.

The chief genus in the Gorteriinæ is *Berkheya*, which has a pappus essentially similar to that of *Arctotis*, but with type G appearing occasionally. The only other large genus is *Gazania*, in which the numerous, narrow setæ of type F are sometimes difficult to distinguish from the hairs of the cypsela. The

tendency to reduction towards type N which appears rarely in the Arctotidinæ is more developed in this sub-tribe, appearing in three genera.

The Gundeliinæ is a small group with the pappus of type F, connate at the base, or the reduced form, type N.

Anthemideæ. The pappus here is usually reduced to the fimbriato-coroniform type when present, but in a large proportion of the genera it is entirely absent. In a few genera, such as *Athanasia, Lepidostephium, Allardia, Isoetopsis,* and *Marasmodes,* the evolution of type N has proceeded only as far as type F, the paleaceous setæ being connate at the base and quite short in several of the above genera. The next step is seen in other genera, such as *Anacyclus, Anthemis, Pentzia* and *Crossostephium,* where the pappus in some species is very short and the fimbriato-coroniform type is more common. In many of these genera and others of the tribe type Qb occurs, *e.g.,* some species of *Chrysanthemum, Cotula, Pentzia* and *Anthemis*; or the pappus may be type N, or type Qb, or absent in different species of the same genus.

Interesting transition forms occur in the various species of the anomalous genus, *Oedera,* types N and F occur in addition to a special form somewhat like type K but with the paleæ fused by their margins to give a deep, membraneous tube, fimbriate at the top.

In only one genus, *Cancrina,* are the paleæ few in number, type M, and in some species of the most closely allied genus, *Allardia,* setæ more or less flattened, but closely approximating the typical pappus of the Senecioneæ, occur. Other species of *Allardia* show these setæ developed into type F, with the length reduced and the setæ connate at the base ; the apex of the setæ may be simple or plumose. In *Allardia* and *Cancrina,* therefore, we get a complete series of transition forms leading from type A to types N and M.

As *Oedera* and *Allardia* are in separate sub-tribes we again get no indication of the relative position of the Anthemidinæ and Chrysanthemidinæ and it becomes probable that the Anthemideæ, like the Cichorieæ, is sub-divided on an artificial basis.

Inuleæ. The Gnaphaliinæ is taken as the primitive sub-tribe and the Helichryseæ as the primitive group within that sub-tribe, the Eu-gnaphalieæ being derived. This arrangement is confirmed by the structure of the pappus. *Helichrysum* and *Gnaphalium* are the chief genera ; the former has one row, or rarely several rows,

of setæ of type A, or occasionally the setæ are barbellate or sub-plumose at the apex, and may be free or connate in various ways at the base. The latter is similar, but the setæ are never in more than one row and sometimes have the cilia of the plumose apex fused, giving thickened and club-like setæ. Here also the setæ are free or connate at the base. The other genera are mostly setose and similar to the above, connation at the base being common and leading to the paleaceous and fimbriato-coroniform types in a few genera of the Helichryseæ.

The barbellate and sub-plumose types of the primitive genera develop in others into types plumose at the base, as in *Helipterum*, or at the apex, as in *Podotheca*, or the setæ may be scabrid, barbellate or plumose, as in *Waitzia*. Types A, D, E, F, G, M and and N occur in this sub-tribe, the primitive types A and D predominating.

Types A and D are characteristic of the Tarchonanthinæ (cp. Fig. 7, Chap. II). The higher types L and K occur in several of the Filagininæ, but this sub-tribe also shows types A and D in two of the chief genera, *Filago* and *Ifloga*, and type N in two smaller genera. The pappus may be absent occasionally in most genera and is never present in several.

Types A and D are again common in the Plucheinæ (cp. Fig. 7), but type E occurs in *Pterigeron* and F in two small genera. The relatively higher type D is commoner in the Inulinæ than in the lower groups (cp. Fig. 7), as are also types E, F and K, while in a few isolated genera the number of paleæ becomes reduced. The pappus may be in one to several rows and is frequently in two, the inner setose and the outer paleaceous.

The Angianthinæ, Relhaniinæ and Athrixiinæ show a very similar range, varying even in the same genus from type A to types K or M, and showing in general the types on the evolutionary lines leading to types I and M (see Fig. 18).

The Buphthalminæ are of special interest as an intermediate group (cp. Fig. 7). Most of the genera have only one or two species and setæ of type A occur only in *Gymnarrhena*. Similar setæ but with the apex barbellato-plumose occur in *Rhanterium*. In the other genera the pappus is either absent or paleaceous of various types. Even in *Gymnarrhena* there is an external row of eight to ten setæ of type F, and in *Rhanterium* the setæ are reduced to four or five. The paleæ in the other genera are usually numerous and short, sometimes fused to give type N, sometimes prolonged into aristæ, as in type G.

Cynareæ. The Centaureinæ is taken as the primitive sub-tribe and in the chief genus, *Centaurea*, we find a wide range of pappus. forms; the setæ are in numerous rows and show various stages in fusion from the inner setæ of type A to the outer short paleæ of type K; types A, C, D, E, F, H, K, L and M occur, some of them in the same species, some of them in different species of this diversified genus. This covers the range in the other genera but these show a more limited variety of pappus forms. The plumoso-setose type is frequent in the Carduinæ but types A, B, C, D and F occur and are frequently connate at the base, a condition which is not common in the Centaureinæ. *Gymnarrhena* is, therefore, a very good intermediate form, leading on to *Centaurea* on one hand and by a similar development of paleaceous setæ to the rest of the Buphthalminæ on the other.

The Plucheinæ were suggested as an alternative source for the Cynareæ (Chap. IV, F), but the pappus of the chief genera in that sub-tribe is of type A, so that it seems more probable that the Centaureinæ, at least, have come from the Buphthalminæ. Polyphyly is, of course, possible and the Plucheinæ would form a probable source of the Carduinæ.

Type E is strongly developed in the Carlininæ but paleaceous types also occur and show a tendency to reduction, *e.g.*, in *Xeranthemum*, where the pappus may be absent or composed of minute paleæ. This leads on to the Echinopsidinæ where the pappus is of types F or N.

Mutisieæ. Here the Nassauviinæ are the primitive sub-tribe. The corolla form of *Nassauvia* (see Fig. 10, Chap. IV), suggests that genus as primitive but the pappus is frequently more or less paleaceous and the genus has a very peculiar habit. *Perezia* and *Trixis* are two of the chief genera and have the pappus of type A ; of these two genera, *Perezia* has a very distinct habit and involucre. while *Trixis* closely approaches *Senecio* in several of its plant forms and in its involucre. It will be noted that the hairs on the cypsela are also very similar (see above Sect. A), and that the style is the same as that of *Senecio*. It only requires a development of basal appendages to the anthers (these appendages are already present in a number of species of *Senecio*) and the development of bilabiate florets throughout the capitulum (which it has been suggested is the effect of excessive nutrition, Chap. IV, C) to change a *Senecio* into a *Trixis*. The mutations necessary for some, at least, of the generic differences in the Compositæ will be seen from this to be

quite small, (cp. the origin of the Cichorieæ from the Senecioneæ, Chap. IV, B).

In the other genera of the Nassauviinæ types D and E are common; type F and a type between E and M occur in *Nassauvia*, and the number of paleæ may be reduced in that genus and is usually so in *Triptilion*. Types E, F and G occur in the Barnadesiinæ and types A-F in the Onoseridinæ. In connection with the suggestion of *Mutisia* as the primitive genus in the latter sub-tribe (see Chap. IV, F), it is interesting to note that the pappus there is the same as the dominant form in the Nassauviinæ, *i.e.*, type E.

The Gerberinæ are suggested to have come from *Mutisia* but type A is the commonest pappus-form in this sub-tribe, while *Mutisia* shows only type F. An allied genus, *Onoseris*, has type A pappus and on this point seems a more probable source. Types D and E also occur in the Gerberinæ. The plumoso-setose type is dominant in the Gochnatiinæ but types A, C, D, K and M occur in a few species. The appearance of the paleaceous types confirms the position of this sub-tribe, but the evidence of all the characters of the florets supports the conclusion that *Mutisia* gave the Gochnatiinæ and *Onoseris* the Gerberinæ.

Vernonieæ. The chief genus in this tribe is *Vernonia*, and the other genera are really more or less sub-genera of this large one. Most of the floral characters point to *Vernonia* being the primitive genus of the tribe and this is also borne out by the pappus. There are usually two, sometimes three, rows of setæ, which are frequently all type A and numerous; the inner row is usually of type A but occasionally of types F or K, and may be free or connate at the base; the outer row is usually of an abbreviated type K but quite frequently is setose scabrid (type A). A reduced number of setæ is present in some species especially in the African and Asiatic sections, or the pappus may be altogether absent. If this range of variation be compared with that of *Senecio* and more closely with that of *Liabum* (see above) the derivation of *Vernonia* from *Senecio* viâ *Liabum* is seen to involve only a few changes in the characters of the florets.

Type A is commonest in the rest of the Vernoniinæ; in a few genera types N, F and K occur and the pappus is occasionally absent.

Paleaceous types are dominant in the Lychnophorinæ, while two of the chief genera frequently show type A but types F and K also

occur in these genera, and the fimbriato-coroniform type is shown by other smaller genera.

Asterea. The Homochrominæ is taken as the primitive sub-tribe; type A is dominant with type D as a common variation and types F and O in a few genera. In the small genus, *Homochroma*, the setæ are plumose, type E. There is also a tendency to abbreviation and connation of the setæ. This same tendency is more strongly developed in the Bellidinæ, leading in most genera to type N or to complete reduction. In the chief genus, *Brachycome*, abbreviated forms of types A and F occur and are sometimes connate, so that it is probable that the Bellidinæ have arisen from the Homochrominæ.

Type A is again dominant in the Conyzinæ and Baccharidinæ, with a tendency to connation at the base in a few genera and the same approach to type F, and more rarely to type E, as occurs in the Homochrominæ.

The five chief genera of the Heterochrominæ are *Aster*, *Erigeron*, *Olearia*, *Felicia* and *Celmisia* and these all show type A. There is, however, a large number of smaller genera in which types D, F or O occur, Types E, N and M occur more rarely. The advanced position of the Heterochrominæ compared with that of the Homochrominæ, which was suggested by the colour of the corolla (Chap. IV, D), is confirmed by the greater development of the types E, F and O in the former sub-tribe.

The pappus is frequently absent in the small sub-tribe, Grangeinæ, and when present is usually of the reduced type N, or an abbreviated form of the fimbriato-paleaceous type K, which is very closely allied to type N.

Eupatorieæ. The primitive sub-tribe here is the Ageratinæ and within the sub-tribe the *Eupatorium-Mikania* group is basal. In these two genera type A is the usual pappus-form; the setæ are frequently connate at the base and type D also occurs rarely. There is a marked tendency to fusion of the setæ, and types E, F, G, K and O all occur. Reduction is sometimes present giving type N, or no pappus at all, or the number of aristæ or paleæ, which varies from many to two, may be reduced to five, ten or twelve. This reduced number of members may or may not be associated with the vascular bundles of the pericarp but when ten or five are usually so associated.

This tendency to reduction shows clearly in *Sclerolepis*, a transition genus between the Ageratinæ and Piqueriinæ (see 61b,

Figs. 3-5), and is continued in the latter sub-tribe, giving 3-5 aristæ in *Adenostemma* and type N in *Piqueria*. Type E which is common in the Ageratinæ also occurs here in three genera and types G and K in other genera. Type A is again dominant in the Adenostylinæ with types D and E as common variations. All three types occur in *Brickellia*, the chief genus, and type G occurs also but only in *Carphochæte*.

Heliantheæ. The aristate type O and its derivatives (see Fig. 18) form the dominant types in this tribe. The tendency to lateral fusion and reduction giving the paleaceous and fimbriato-coroniform types are also present, but to a smaller extent.

The Verbesininæ is taken as the primitive sub-tribe and frequently shows only two aristæ; that this is a reduced not a primitive pappus-form will be clear from the above account of the pappus (Sect. B) and this view is supported by the fact that the other reduced form, type N, is also of frequent occurrence in this same sub-tribe, and also by the fact that the pappus is frequently absent altogether. The setose origin is further demonstrated by the frequent presence of paleæ of types K and L (which are clearly fused setæ) between or among the aristæ, and by the *Helianthus* type, which is type N, with two of the major lacerations larger than the others, thus passing locally into type K.

The pappus is absent from the Ambrosiinæ, except in one genus, *Dicoria*, which shows a feebly developed type N structure. In the Petrobiinæ the pappus is absent or of type N in combination with 2-4 structures of type G. This same combined type, where a few of the fimbriations of type N become thickened and elongated, thus passing locally into type G, occurs in the Lagasceinæ.

The Zinniinæ usually have the pappus absent, but type O is present occasionally. The Coreopsidinæ are characterised by type O frequently developing into types Pa and Pb or being reduced to types R or Qa. The pappus is also sometimes absent, so that the tendency to reduction reaches its extreme expression.

This tendency to reduction is developed further in the Melampodiinæ, the pappus here being frequently absent, and showing only types R, Qa and N when present, except in a few cases where types O and G occur.

The tendency to reduction is even more accentuated in the Milleriinæ (cp. Fig. 7), where in most genera the pappus is entirely absent, showing type N in only two genera and four aristæ of type O in another genus.

The affinity between the Galinsoginæ and Madiinæ which is

suggested in Fig. 7 is emphasised by the pappus characters. In the Galinsoginæ the tendency to lateral fusion shown in the Verbesininæ is further developed, the pappus being usually of types G or M. The Madiinæ have more in common with the Coreopsidinæ in that type N is dominant, but type G occurs in *Wilkesia*, and occasionally in *Layia*, which genus also shows type E, which it will be remembered gives type M (see Figs. 17-18). Type K also occurs occasionally in *Achyrachæna*.

Helenieæ. The tendency to lateral fusion of the setæ which shows in the Galinsoginæ becomes dominant in the Helenieæ. Types A and D occur within this tribe only in the Tagetinæ, which is taken as the primitive sub-tribe, but as these types are practically absent from the Heliantheæ their presence in several of the Tagetinæ raises the question of the origin of that sub-tribe.

There are several possible explanations; the most probable one is that the reclassification of this tribe is required. The Helenieæ, like some of the other tribes, is not a very natural group; indeed, Bentham put forward this tribe with some uncertainty (cp. 5, p. 381). It is distinguished from some of the Heliantheæ only by the absence of paleæ from the receptacle, and the genera with the pappus setose are practically Senecioneæ in all their characters, except the slight tendency of the setæ to be paleaceous at the base. This, it has been pointed out above occurs even in the genus *Senecio*, but Bentham seems to have been unaware of the act.

Apart from these anomalous forms the Tagetinæ usually shows type G, but types K and L also occur. The Flaveriinæ are a small group with type G or the reduced type N or no pappus at all. The Heleniinæ are usually type G, but one genus, *Trichoptilium*, shows type L, and another, *Psathyrotes* (removed to the Senecioninæ by Hoffmann) shows B.

The Baeriinæ usually have the pappus of type G, but a consider_able variety occurs which it is unnecessary to discuss in view of the contemplated reclassification of the tribe. The chief point to note is the appearance of type N in a number of genera and the complete absence of the pappus in a number of others. This leads on to the stronger development of type N in the Jaumeinæ, cp. Fig. 7.

D. Phylogenetic Significance of the Pappus.

The spasmodic variation of the pappus in related genera has been pointed out in Section A, but the pappus-forms when treated on broad lines as in Section C are capable of yielding valuable

phyletic data, provided that critical tendencies are considered to be
of as much importance as actual form. Two such tendencies, *i.e.*,
cohesion and reduction which are fundamental tendencies in the
other parts of the floret, can be recognised as being ruling factors
in the development of the paleaceous, aristate and coroniform types
from the primitive setose types. These lines of orthogenesis are the
key to the otherwise hopelessly confused mass of variations shown
by the pappus.

Many of the points where the pappus-form has a phyletic value
have been indicated in Section C so that it is only necessary to
summarise briefly the phyletic value of this part of the floret.

Senecio is confirmed as the basal genus, by the dominance of
the most primitive pappus-forms and the occasional expression of
the two fundamental tendencies above-mentioned. The basal
position of the Senecioninæ is also confirmed by the same facts
and the lines of evolution leading to the higher types of pappus are
traced in outlying genera.

The Liabinæ are confirmed as an intermediate stage in the
development of the Vernonieæ and the derivative position of the
Lychnophorinæ is also verified.

The origin of the Cichorieæ from the Senecioninæ is confirmed
and the progressive development of the two critical tendencies
together with the frequent presence of the primitive types is clearly
shown.

There is also evidence in support of the suggested origin of the
Calenduleæ as a reduction product of the Senecioninæ.

The evolution of type M from type E occurs in the origin of the
Arctotideæ, *Ursinia* again being the basal genus, with the Gorteriinæ
as a progressive variation and the Gundeliinæ as a reduced
derivative.

In the Anthemideæ the tendency to reduction is more strongly
developed, leading to the frequent absence of the pappus or its
presence in the form of type N. The occurrence of transitions
from type A through F to N is evidence in support of the suggested
origin of this tribe from the Senecioninæ.

The Inuleæ show a very marked progressive evolution in the
pappus forms from the Gnaphaliinæ (type A usually) to the Inulinæ
(types A, D, E, F and K), with type A passing into types D, E, F and
G in the Buphthalminæ leading to the Cynareæ, where the higher
setose and paleaceous types are well developed

In the Cynareæ *Centaurea* is confirmed as the primitive genus,
with the positions of the Carduinæ, Carlininæ and Echinopsidinæ

as in Fig. 7. The possible polyphyletic origin of the Cynareæ is suggested and the Plucheinæ are indicated as a possible alternative source of the Carduinæ.

The most interesting point is the confirmation of the origin of the Nassauviinæ from the Senecioninæ and the primitive position of that sub-tribe in the Mutisieæ. *Trixis* is clearly the primitive genus; this is confirmed by the character of the achenial hairs. *Mutisia* is confirmed as the primitive genus in the Onoseridinæ, with *Onoseris* as a closely allied basal genus giving the Gerberinæ, while *Mutisia* is the source of the rest of the Onoseridinæ and of the Gochnatiinæ.

The rearrangement of the Homochrominæ (Astereæ) below the Heterochrominæ is confirmed. The positions of the other sub-tribes are also supported by the evidence derived from the pappus with the exception of the Bellidinæ, which it is suggested were derived from the Homochrominæ, not independently as in Fig. 7.

The origin of the Eupatorieæ from the Astereæ by the passage of the Heterochrominæ into the Ageratinæ and the position of the *Eupatorium-Mikania* plexus at the base of the latter sub-tribe are upheld by the present evidence, as is also the passage of the Ageratinæ into the Piqueriinæ via *Sclerolepis, Adenostemma,* and *Piqueria.*

The Helantheæ again show advanced characters, the tendency to fusion in clumps and reduction being well-developed in the primitive sub-tribes, while the tendency to lateral fusion of the setæ culminates in the paleaceous forms of the Galinsoginæ.

The possibility of the Helenieæ being an artificial group is indicated and a close affinity of many of the genera with the Senecioninæ is traced, while the evolution of the sub-tribes is left for future consideration on account of the variation in the form of the pappus.

It is clear, therefore, that the consideration of the pappus in the light of the evolution of the various types from the primitive setose form confirms the previous phyletic suggestions in most of the more important points, and even furnishes valuable indications of the more detailed evolution of certain groups such as the Vernonieæ, Eupatorieæ, Cynareæ and Mutisieæ.

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THE RECONSTRUCTION OF ELEMENTARY BOTANICAL TEACHING.

"STICK TO IT!"

To the Editor of the NEW PHYTOLOGIST.

DEAR SIR,

Recently I happened to pick up the number of your journal containing "The Examination of a Witness," and its form and subject, unusual in a scientific periodical, attracted my attention. So much interested was I, that I got hold of the preceding number containing "The Reconstruction of Elementary Botanical Teaching" and read it through. As a free lance now, though not without some experience of both teaching and being taught I cannot refrain from contributing to your discussion.

Well, Sir, first of all I congratulate you warmly on having "belled the cat." What you have said wanted saying and wanted it badly. Whether it will have any practical result is another matter. If it is generally received in the spirit of "Witness" it certainly will not. He avoids meeting the essential points of your case and falls back on the stereotyped justification of the elementary course devoted mainly to comparative morphological detail. His claim that such detail represents "the fundamentals of pure botanical science" is really astonishing at this time of day. His statement that you advocate "short cuts to the useful at the expense of thoroughness" is not based, so far as I can discover, on anything in your article, the whole of which is a plea for concentration on fundamentals. The demand for "a new spirit and a new ideal" evidently annoys "Witness" acutely, and yet these are exactly what we want. He is right in saying it "recalls the exhortations of preachers of other doctrines than those of natural science." A conviction of sin and a change of heart are what you and your co-signatories are seeking, but if your appeal and the circumstances of the time together have no effect, I fear you will have to look elsewhere for development, and the disruption of botany, which you justly anticipate, may

very well complete itself, for the science of plants is certainly not doing its duty to the country.

The great practical difficulty in carrying out reforms such as you advocate seems to me to be the absence of the men to carry them out. The few bright young men who are interested in what matters and who have survived the morphological mill, naturally have no chance of settling what shall be taught, and from the people in established positions, apart perhaps from your co-signatories, it does not look as though you would get much help. Still if you can get the things that matter constantly held up before the teachers you may get a gradual change in the right direction. How would it be to ask those (and I imagine there are some) who are trying to teach on more fundamental lines to publish their syllabuses? Would it be possible to get out an elementary text book of the right sort? Is there anyone who could and would write it, or would co-operation be possible?

These few halting suggestions are, I am afraid, all I have to offer by way of constructive proposals. In conclusion I would say: Do not be discouraged by apathy and the *non possumus* attitude which you are certain to meet. Your theoretical position is so eminently sound that in the long run it must commend itself, except to those whose minds have become ossified. I follow the example of " Witness " and sign myself

<div style="text-align:right">Yours pseudonymously but faithfully.</div>

<div style="text-align:right">AJAX.</div>

SOME CRITICISMS AND SUGGESTIONS.

To the Editor of the NEW PHYTOLOGIST.

SIR,

Most Botanists will probably be in agreement with the fundamental criticisms of present-day botanical teaching that the treatment is too largely morphological and phylogenetic, and takes too little cognisance of physiology. But when one turns to the translation of general principles of improvement into practice several obvious dangers present themselves. The time is not so very remote when botanical teaching was as much dominated by the taxonomic point of view as it now is by the morophlogical. Taxonomy however at the present day only forms a very small part of the botanical curriculum, but, nevertheless, far from this being accompanied by a better and more fundamental treatment, there is probably no part of the subject which is more inadequately taught. The restricted time available for systematic Botany is usually devoted to the study of certain groups that are

required by some syllabus, and the average student, after taking a "Pass" degree, is not merely unacquainted with many common plants, but as a rule is quite incapable of utilising a flora to the best advantage. This is the more to be deprecated since, in the fields of economic and applied Botany generally, the importance of critical forms, as distinct from the larger aggregates, is becoming more and more emphasised.

It is therefore manifestly important that the contemplated curtailment of morphological studies should not be open to the same objection and result in a barren remnant of little educational value. The necessity of a sound morphological training cannot be too strongly emphasised, for, whether the student proposes ultimately to follow ecology, physiology, or applied Botany in its many branches, a thorough acquaintance with plant-structure is a necessity, not merely for the proper comprehension of the problems which nature affords, but also as a safeguard against viewing the plant as a mere aggregation of chemical and physical phenomena. The sterility of morphology and taxonomy is largely, if not entirely, an outcome of the fact that they are taught as ends in themselves and not as essential tools in the mental equipment of the student. As a consequence we find at the present day that many of those engaged in applied Botany are very inadequately trained in these respects.

To a large extent the ecological view-point will, with its comprehensive vista, afford a corrective to this attitude, but the general introduction of ecology into the elementary course (especially in the first year) is not devoid of danger in the hands of inexperienced teachers. Many of the results of ecology are as yet necessarily tentative, and as such are not suited for presentation, except to a mind already trained to critical consideration. The complex of factors involved in the relation of plants to their environment is only beginning to be unravelled and, as a consequence, there is a risk, well exemplified in current ecological literature, of regarding problems in the light of single factors, rather than as the resultant of the inter-action of many. Nowhere perhaps is this criticism more pertinent, or the inadequacy of our knowledge more patent, than in the domain of autecology, and therefore we regard with some misgiving the suggestion (Memorandum, p. 246) that the elementary course should embrace " a treatment of the physiological life history of the individual plant."

With due recognition of these difficulties we fully support the

suggestion that ecology in the broadest sense, together with its bearing on agriculture, horticulture, and forestry, should occupy a prominent position in the elementary curriculum, and that the physiological conception should be infused into morphology and anatomy.

We feel that one of the great faults of morphological teaching at the present time is the retention of details that are comparatively irrelevant. As instances we may cite the details of archesporial development, comparative stelar anatomy (especially in the Pteridophyta), the methods of segmentation in meristematic tissues, the details of flower and fruit structure in Angiosperms (which are readily acquired in the use of a flora), the cytological details of Fungi, etc. On the other hand morphological training, for pure and applied Botanists alike, should include a thorough grounding in the essential characters of the chief groups of the Vegetable Kingdom. The course of lectures dealing with this part of the subject could be relatively brief, but the practical work should be of such a nature as to enable the student to determine the approximate systematic position of any form which might come within his purview. That is to say the training should be a preparation for the acquisition of knowledge to meet future requirements and not the mere assimilation of a large number of facts.

In the domain of physiology we support the recommendation of Mr. T. G. Hill that students should be encouraged to devise and construct their own apparatus wherever feasible. In view of the importance to be given to ecology and the economic trend a moderate-sized garden should be available for experiments on the living and undisturbed plant. The general principles of cultivation, of the application of manures, etc., should be tested by the students themselves on suitable plots in this garden. Nothing is better calculated to inculcate the practical application of physiological principles than the actual cultivation, on the part of students, of a small area of ground.

Any change in the teaching of Botany which is to be not merely temporarily effective must aim at the removal of the domination of the lecture-room and laboratory by the examination. To this end the syllabus should lack rigidity and thus leave scope for the individuality of the teacher. It is desirable too that there should be accompanying modifications in cognate subjects (*e.g.*, Chemistry and Physics), so that courses in these latter dealing

with those aspects more especially concerning the biologist might be available. The suggestion that each department should have a physicist and chemist attached is an ideal that will probably at present prove not to be within the scope of practical policy.

We fully agree with Mr. T. G. Hill that the different subjects should be taken consecutively and not concurrently, all the more as other laboratory subjects (*e.g.*, Chemistry and Physics) form the best adjuncts to Botany. We also endorse the view that a Pass degree should be a necessary step to graduation in an Honours school. As regards the subjects for the former, we should deprecate too restricted a choice of combinations, since for some morphological minds it is conceivable that, for instance, Botany, Zoology, and Geology might yield good results. For this reason too the suggested Honours schools, namely Physiology and Ecology, Biochemistry and Biophysics, and Morphology are open to objection, since in the case of an agricultural student, for example, the grouping of Ecology and Biochemistry would probably be more advantageous than any other.

<div style="text-align:center">We are, Sir, etc.,</div>

<div style="text-align:center">F. E. FRITSCH.</div>

<div style="text-align:center">E. J. SALISBURY.</div>

A SUGGESTION FOR AN HONOURS COURSE.

To the Editor of the NEW PHYTOLOGIST.

SIR,

That the university teaching of botany needs vitalising can scarcely be doubted; and we owe a great debt to the NEW PHYTOLOGIST for raising the question in such a practical manner. As the matter is being discussed, I venture to put forward an alternative proposal.

It will readily be granted that botany is now too large a subject to be covered adequately in a two years' course. Some form of specialisation is clearly necessary; and yet I cannot regard without misgiving the division of botanical learning into three schools. We cannot look back without envy on our ancestors who were able, not so very long ago, to have a fair working knowledge of the whole of science, whilst today, most of us have an adequate acquaintance with only one department of it. Need we carry the process a stage further and condemn our botanical descendants to a

comparative ignorance of the methods and aims of two-thirds of botany?

The alternative I have in mind may be explained by the following outline of a syllabus. The preliminary course should be as general as possible, covering more physiology and ecology than is usual at present, but containing also a good general survey of the main groups of plants and their inter-relationships. It should be separate from the course for the pass degree, which has a totally distinct object, and if this is conceded, the morphological basis may be retained in the preliminary course.

The second and more important part of the course should consist primarily of a very thorough and special study of a small number of types, say four, taken from different phylogenetic or ecological groups. All, or nearly all of these must be British plants which the student can study *in situ.* He should himself bring specimens into the laboratory, pickle what is necessary, grow what can be grown, perform physiological experiments on them, and gain as thorough a knowledge of them, morphological, physiological, ecological and phylogenetic, as is possible in the time. He will need to know the more important original papers which bear on the subject, and text-books will take their proper place as books of reference and bibliographies. The student will be encouraged to follow those lines of investigation which are peculiarly suggested by each type, but he should be expected to make quantitative determinations of assimilation, respiration and transpiration on at least some of his types.

I do not want to labour the advantages of this system, but I hope your readers will consider it as a possible method of specialising and at the same time covering more branches of botanical science than is usual at the present time. A special point which may be advanced in its favour is that students who intend to apply their knowledge of botany to forestry, agriculture or the like, can partly select as their types species which will be of eventual interest to them as crops, weeds or parasites.

In addition to his types each student should have to take three or more special subjects chosen from a list including plant metabolism, plant movement, ecology, genetics, cytology, paleo-botany, history of botany, biochemistry, and perhaps the larger groups, Fungi, Algæ, Bryophyta, etc. His knowledge of these subjects could be examined in the ordinary way and a higher quality might be expected as further specialisation is allowed.

That the position of examiners would become more difficult must be admitted. However, man is not made for examinations, but examinations for man ; and even those who do not hold with the popular outcry against the examination system could not discourage the adoption of a good method of botanical teaching on the ground that it would render less exact the examiner's classification of students. In any case the difficulty is not insuperable.

That the system would make it easier for the shirker to shirk is not a serious objection. We have to work for the better half of the students, rather than the worse, and at present far too much of the teacher's energy is taken up with looking after the consciences of students who have not got any ; and a conscience is far more likely to be generated by a curriculum which encourages the maximum of interest than by the constant application of a moral *force majeure.*

<div style="text-align:center">

I am, Sir,

Your obedient servant,

W. E. HILEY.
</div>

49, Glenhouse Road, Eltham.
    24th February, 1918.

WANTED THE FACTS AS TO WHAT IS ACTUALLY TAUGHT.

To the Editor of the New Phytologist.

Sir,

In connection with the memorandum on the Reconstruction of Elementary Botanical Teaching I venture to express some opinions, and to offer some suggestions which I hope may be considered practical.

The memorandum is very vigorously worded, and can hardly fail to convey the impression that British Botany is in a very parlous state indeed, and that this is attributable almost entirely to the nature of current elementary curricula, with regard to which it is urged that the study of plants from the point of view of function and relation to environment is practically neglected.

Now it appears to me that in view of the activity of the " Nature Study " movement during the past decade, resulting in the publication of numerous volumes dealing with plants essentially

as living organisms, in the fairly wide introduction of school gardening, with the carrying out of the observations upon the growth of plants indoors and in the field, and the performing of simple physiological experiments with homely apparatus, all of which has not been without effect upon the nature of school, matriculation, college entrance and higher examinations, there is perhaps some room for doubting if the preponderance of pure morphology without reference to physiology is really so marked and so widespread a feature of elementary botanical teaching in British Universities as the memorandum insists.

The matter is one calling for a fair investigation, and I would therefore suggest that steps should be taken to prepare a report upon current botanical instruction in every institution of University rank throughout the United Kingdom. In the case of each department the report might refer to the following subjects:

1. *Staff*—number, academic qualifications, experience, researches, salaries, superannuation schemes, responsibility for and time devoted to teaching.

2. *Curriculum*—indicating as far as possible the relative proportions of the subject matter, and the scope of " Pass " and " Honours " Degrees both in Botany and in Science as a whole. A list of " types " studied in the elementary courses would be useful.

3. Average number and composition of students.

4. *Teaching*—any special features, *e.g.*, seminars, minor research exercises, theses, plant collecting, discussion societies, excursions, etc.

5. *Accommodation*—for students and staff.

6. *Financial assistance available*—for library, apparatus, studentships, etc.

7. *General facilities* — libraries, plant houses, herbaria, gardens, access to suitable plant communities, marine laboratories, museums, etc.

8. Special facilities for research.

9. Nature of local difficulties standing in the way of progress.

The compilation of such a report would only be possible with the cordial co-operation of the staffs of the departments concerned; its preparation might be expedited if some uniform scheme were agreed upon, so that data could the more readily be tabulated for comparison.

A report of this type would in the first place help all who are interested in the matter to estimate the extent to which the charges made in the memorandum against those responsible for elementary botanical teaching are really justifiable; at present it is difficult to do this.

In the second place it would reveal the facilities, or lack thereof, actually existing for the carrying out of any particular type of curriculum at each of the institutions in question.

It would also be of great service to botanists as a whole when action is taken to influence public opinion or government departments with a view to securing grants, concessions, etc. To individual departments it would be of some assistance when negotiating with local College or University authorities.

For these reasons among others I am inclined to think that the preparation and publication of such a report before taking other action, would be preferable to attempting to frame a standard elementary curriculum and subsequently submitting it to botanical departments in general for their acceptance, or otherwise.

There is another point on which I should like to express an opinion, *viz.*, that while the suggested reconstruction of elementary curricula where thought necessary might render considerable assistance, yet by itself this is not likely to effect the results aimed at by the writers of the memorandum. To achieve such ends, to link up the schools with outlets on practical life, etc., it is essential that not only the botanists but the University science teachers as a whole should co-operate.

It is useless to shut one's eyes to the unfortunate existence in the past of inter-departmental jealousies, and without proper co-ordination at each institution some very serious difficulties might arise.

But further than this, if in the case of botany the students trained are to have a reasonable chance of passing into some sphere of work in which their training will be of direct value, there must also be some form of co-operation between botanists and workers in various related branches of science, especially on the applied side. This co-operation should extend to employers, for upon them largely depends the demand for trained people. In short it would seem that the writers of the memorandum have made out a case for the uniting of scientific workers of almost all kinds, and indeed it is more than probable that only by this means can a sufficiently powerful driving force be provided by

which public opinion may be influenced, and a market created for the students it is proposed to equip.

In this connection, too, the letter by Mr. J. J. Robinson on " The British Association and the Nation " (*Nature*, March 21st, page 45), is deserving of the earnest consideration of botanists. Few will deny that the public will need a good deal in the way of propaganda before it forms anything like a clear notion of the aims and ideals of scientific botany. It would be a great opportunity lost if no effort were made to carry out the suggestion contained in the letter in question.

With reference to qualifying for a " pass " degree in science I am very strongly of the opinion that more than one academic year should be spent over botany, especially if it is run concurrently with other subjects. To organise for students with no previous training in botany a complete one year course suitable for a pass degree in a modern University, when other subjects are being studied during the same time, appears to me to be a superhuman task.

The handicap imposed upon the University science teacher by the complexity of the time-table is frequently very severe, especially in the case of the botanist, so much of whose material is living and largely dependent upon the season, instead of being conveniently obtainable at all times from a bottle or shelf, as is the case with the chemist and the physicist.

A great boon would be conferred on both teachers and students if by means of more co-operation between the different science departments greater continuity of practical work could be secured. It frequently happens that even small classes have to be taken in relays, owing to some of the members being unable to fit in their times.

The difficulties are obviously great, but is there no hope that some improvement might be effected if all concerned endeavoured to ascertain the different ideals, working requirements and points of contact of each science, and concentrated upon obtaining a degree curriculum duly balanced and related to the needs of the day and the capacities of the students ?

I am, Sir,

Your obedient Servant,

SYDNEY MANGHAM.

BOTANICAL BOLSHEVISM.

To the Editor of the NEW PHYTOLOGIST.

Sir,

A manifesto on " The Reconstruction of Elementary Botanical Teaching " has been published over the names of five well-known botanists. With much that it contains there will be general accord : the aspiration for more " vitality " is laudable: its end will appeal to us all. The means proposed to obtain that end, and the statements as to the present deficiencies in method and outlook, which stimulated the production of the manifesto, are a different matter. They will not carry the same unanimity.

Two propositions seem to contain the pith of this encyclical :—

(1) That in the present elementary courses Plant Physiology is taught as a separate subject. The teacher does not present the plant as a living organism " because the teaching is mainly in the hands of men who are primarily morphologists " (p. 242).

(2) That in order to secure improvement, " comparative morphology should be reduced to a subordinate position " (p. 251).

These propositions imply an antithesis between Physiology and Morphology, which morphologists in the vital and living sense· will not admit. They teach Organography, which interprets form and function as inter-dependent, so fused that the twain are one flesh. In fact, they endeavour, as I have always done, to present to an elementary class the *Living Plant.* To such teachers the antithesis does not exist, and ought not to exist in elementary teaching : so that the whole discussion is, in their view, proceeding on false premises, so far as it affects elementary teaching. I have always started from Flowering Plants because they give a better chance of introducing simple experiment, and demonstration of vital phenomena on the Lecture Table to a large audience.

Here I must allude to the difficult problem of large practical classes. To introduce individual physiological experiment into a laboratory of over 100 students at one time, where each place may be occupied more than once in the day, and with a limited demonstrating staff would be futile. Observations of form and structure can be more effectively carried out under such conditions. This simple fact accounts for some of the shortcomings that grieve the signatories. I do not see in their manifesto any suggestion that would meet this very real difficulty.

Those who teach the Living Plant in the way described will particularly resent the explanation that the alleged deficiency

arises " because the teaching is mainly in the hands of men who are primarily morphologists." Before applying such a gross assertion generally, the signatories should have taken steps to be better informed than they appear to be. They refer to the attempt some 20 years ago to separate plant physiology from morphology, and to combine it with animal physiology in a distinct section of the British Association. Younger botanists are reminded that it was the morphologists who revolted: and it was a morphologist who proposed the motion that the study of plants should be maintained as one subject. Does it not then seem inconsistent for the signatories now to assert that the faults they allege lie with the morphologists?

Should not the signatories consider whether the cause of their dissatisfaction does not really lie in their own presentment of that functional branch which they put in antithesis to its natural foundations in form? I make no assertion on so delicate a point. But I recommend that the signatories should " diligently try and examine themselves" before they take action. They would do well instead of dwelling on the alleged deficiencies to seek inspiration in the converse picture of that morphological success which they admit. The signatories are complimentary to the British School of Morphologists. But I, who personally have seen more of its history than any of the signatories, deny that it " derived its inspiration and opportunity from the revival of the study of fossil plants." The true history is written in the lives of more than one of our leading Botanists. They show that the thesis should be inverted, *viz.*, " that the study of fossil plants received its inspiration from the revival of morphology, which was already well advanced." It was based on Hofmeister, Sachs and de Bary, whose work prepared the way for the great evolutionary outburst in Britain. Its existence and its success were rooted in the enthusiastic interest of its votaries. Many of them entered Botany as an obsession rather than a profession. Their enthusiasm caught the generous student-mind, and this may in some measure account for the result that the signatories state as existing in some centres, and deplore. I would advise them to learn from this success how a like success in physiology may be attained. That end should be pursued by a natural fostering of interest, not by aggressive or repressive measures.

But instead of such a natural method as this the signatories appear to advocate immediate *Botanical Bolshevism.* They

propose that in order to secure improvement " comparative morphology should be reduced to a subordinate position " (p. 251). I confess such a dictum from scientific men takes my breath away. I hope it is only a slip of the pen, and that they really mean " co-ordinate " and not " subordinate." But five cultivated minds have committed themselves to the latter word. In order to secure their own Utopia they propose to " subordinate " something which they admit is good in itself. That is the spirit that has ruined Russia, and endangered the future of civilisation. Are the signatories prepared to follow a like course ?

Co-ordination between the several branches of a science, as they emerge in the higher teaching, seems to be the only proper basis of advance. I agree to co-ordination of morpoholgy and physiology in advanced work, however little they can be separated in the elementary. These and other branches of the science should start equal and combined, as they now do in the north. Let the signatories then construct by their own enthusiastic work instead of attempting to destroy. The energy of their protest should be transmuted into fresh effort. I would say to them " Physician heal thyself."

Meanwhile another author proposes a committee " to agree on a course of action": the result to be communicated to the teachers of each University. None of us should be so self-satisfied that he would rule out all suggestion for improvement in the balance or character of his teaching. If such a Committee were formed, and I were privileged to see the results of its work, I should give them full consideration. Probably they would not affect my course material-ly, for it is already adjusted to the immediate conditions. The document would then find its way to the goal of many documents —better and worse. In other words, I think such a Committee without powers to standardise teaching would be superfluous, or one might also say impertinent : and I sincerely hope that powers of standardisation will never be acquired. Informal conversation, or perhaps even talking in ink like this discussion, will give better results. Finally, each teacher, with a due sense of his responsibility, and of his opportunities and requirements, must form his own scheme to meet his own needs. If he cannot do this, he is not fit for his position.

<div align="center">I remain,

Yours faithfully,</div>

GLASGOW,   F. O. BOWER.

April, 1918.

ON TURGESCENCE AND THE ABSORPTION OF
WATER BY THE CELLS OF PLANTS.

By D. Thoday, M.A. (Cambridge).

[With One Figure in the Text.]

SO much has been written concerning osmosis in plant that it would appear at first sight superfluous to discuss in any detail the conditions which govern osmotic equilibrium in turgescent cells and tissues. Nevertheless the full significance and implications of the elementary treatment of this subject appear to be by no means generally understood. Lepeschkin[1] has dealt in some detail with the equilibrium relations of cells to water and solutions in connection with his interesting researches with *Pilobolus* and *Spirogyra*, but his papers are not as well known as they deserve to be. Renner's[2] admirable papers on transpiration from the point of view of the cohesion theory contain thoroughly sound discussions of the relation of suction force to osmotic pressure. But with few exceptions those who have worked in this field either have not fully understood the subject or have regarded it as too elementary to need dealing with in detail. Even in Livingston's " Rôle of Diffusion and Osmotic Pressure in Plants " there is no perfectly clear and explicit treatment of the equilibrium of a cell with solutions or other cells in contact with it ; and his reservation of the term turgor " to express the osmotic pressure of the internal fluid " seems to the writer particularly unfortunate.

These problems are fundamental to the whole question of the water relations of plants ; yet the inadequate or even misleading treatment of them in existing text-books makes this important subject one of special difficulty to the student. The discovery, to which reference has been made in an earlier paper,[3] that workers like Stiles and Jörgensen, who have shown themselves clear sighted and critical in other directions, have not succeeded in freeing their minds from the misconception that a solution in which a turgescent tissue shows no gain or loss of water is isotonic with the cell-sap,[4] forces the writer to the conconclusion that inadequate views are still widely prevalent.

That such a use of the term isotonic is unjustifiable is obvious when one considers that submerged fresh water algæ are normally in an essentially similar condition of equilibrium which could not be described by saying that their *sap* is isotonic with water !

It is however not sufficient merely to realise an error of this

[1] Bot. Centralblatt, Beihefte XIX, 1, 1906, pp. 425 *et seq ;* Berichte d.d. bot. Ges., XXVIa, 1909, p. 198 , etc.

[2] Flora, 103, 1911, p. 171.   [3] New Phytologist, 1918, p. 57.

[4] " Studies in Permability," Ann. of Bot., 1917, pp. 425, 426,

kind, for it has subtle ramifications which often vitiate discussion of the osmotic relations of transpiring leaves, of the passage of water through tissues, and of other similar questions.

It has therefore seemed desirable to attempt a brief elementary exposition of the conditions which govern the equilibrium of a cell with a watery solution and with other cells; and to illustrate the consequences by applying them in some important cases.

Osmotic equilibrium in turgescent cells.

In all applications of physical and chemical principles to the analysis of complex physiological phenomena a clear understanding of their action in simple cases is an essential preliminary to the consideration of observed complications or discrepancies. The old explanation of turgescence associated with the names of de Vries and Pfeffer is essentially a simplified approximate description of the phenomena, and in this sense will always hold good. Whatever the ultimate explanation of osmotic pressure, permeability, imbibition and other factors that may have to be reckoned with in an exhaustive analysis, there can be no doubt that osmotic pressure, acting against an elastic cell wall, plays the chief part in developing and maintaining the turgor so characteristic of vacuolated plant cells and tissues. In the first instance we may therefore ignore the swelling of the colloidal constituents of the cell.

If an isolated cell is placed in water, water enters it and distends the cell-wall. The wall is elastic, in the sense that it resists extension (though it is not inextensible)[1] and within certain limits does not suffer permanent extension but is capable of returning to its original dimensions on removal of the stretching force.[2] The distended wall compresses the protoplasm and sap, in which the consequent hydrostatic pressure (called by Lepeschkin " Turgordruck," or turgor pressure) is equal and opposite at any moment to the inward component of the tensions in the wall. This turgor pressure tends to force water out of the cell. When swelling is complete and equilibrium reached the turgor pressure balances the osmotic pressure of the sap. In this condition the cell is *fully turgid;* it is in equilibrium with water; and it is *incapable of absorbing more water* so long as neither the osmotic pressure of the sap nor the tensions in the wall[3] suffer

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[1] Stiles and Jörgensen have confused elasticity with extensibility—*l.c.*, p. 420.

[2] How far this is strictly true still requires critical investigation. It is probable that hysterœsis is shown, and even some degree of plasticity, by thin cellulose walls, but hitherto the time factor has been left out of account in investigations on the elasticity of plant tissues.

[3] *E.g*, by growth (intussusception) or owing to some degree of plasticity under prolonged strains.

change. If we represent the turgor pressure by T, and the osmotic pressure by P, we can express this condition by the equations

$$P = T \text{ or } P - T = O.[1]$$

The water-absorbing power of a cell.

We have seen that a fully turgid cell is incapable of absorbing more water. If, however, the cell be removed from water and left for a time exposed to the air, it will lose water by evaporation and become less turgid: in other words, as the volume diminishes the cell wall is less distended and the turgor pressure correspondingly falls. At the same time the cell becomes once more capable of absorbing water if it should be replaced in water. In this condition $T < P$ and $P - T > O$.

The expression $P - T$ represents a quantity of very great importance in any consideration of the water relations of plants, but one for which there is no recognised term. It is that part of the osmotic pressure of the cell sap which is not balanced—and so neutralised from the point of view of water absorption—by the turgor pressure. It is thus the net force tending to bring about the entry of water. We may for the present call it simply the *water-absorbing power of the cell* to distinguish it from the full osmotic pressure of the cell sap. If we represent it by p, we have $P - T = p$ as a general expression for the condition of a cell, viewed as a simple osmotic system.

That this expression requires further elaboration is obvious; but whatever complications may enter into the further analysis will not invalidate it. It must always remain true that the inward pressure of the distended cell wall is balanced by the hydrostatic resistence of the compressed fluid within; and that the force with which water tends to enter, whatever the explanation of it, is progressively antagonised as the turgor pressure increases.

We may now consider the case of a cell immersed in a solution. In this case the water-absorbing power of the cell is opposed by the osmotic pressure of the surrounding medium. If no flow of water occurs in either direction the cell is already in a condition of equilibrium with the solution. Clearly in this case we may represent the equilibrium by the equation

$$P' = p = P - T$$

where P' is the osmotic pressure of the solution outside. Thus, *the osmotic pressure of this solution is a measure of the water-absorbing power of the cell.* Moreover, *the solution will obviously be isotonic with the cell sap only when* $T = O$, *i.e., when there is*

[1] Expressing magnitude only, not direction.

no turgor pressure.[1] This is the condition which was used by de Vries in his plasmolytic method of determining isotonic coefficients ; for he determined the strength of solution which just began to plasmolyse the cells, *e.g.*, of the coloured epidermis of *Tradescantia discolor.*

The relations between the various factors are represented in graphic form in the accompanying diagram, in which the osmotic pressure of the sap, the water-absorbing power of the cell and the turgor pressure are plotted as ordinates against the volume of the protoplast, which diminishes from left to right, or the " saturation deficit " which increases from zero in the same direction.

osmotic pressure of cell sab (P)

water-absorbing power (p)

turgor pressure (T)

Diminishing volume of cell ⟶

cell wall not distended : turgor pressure nil.
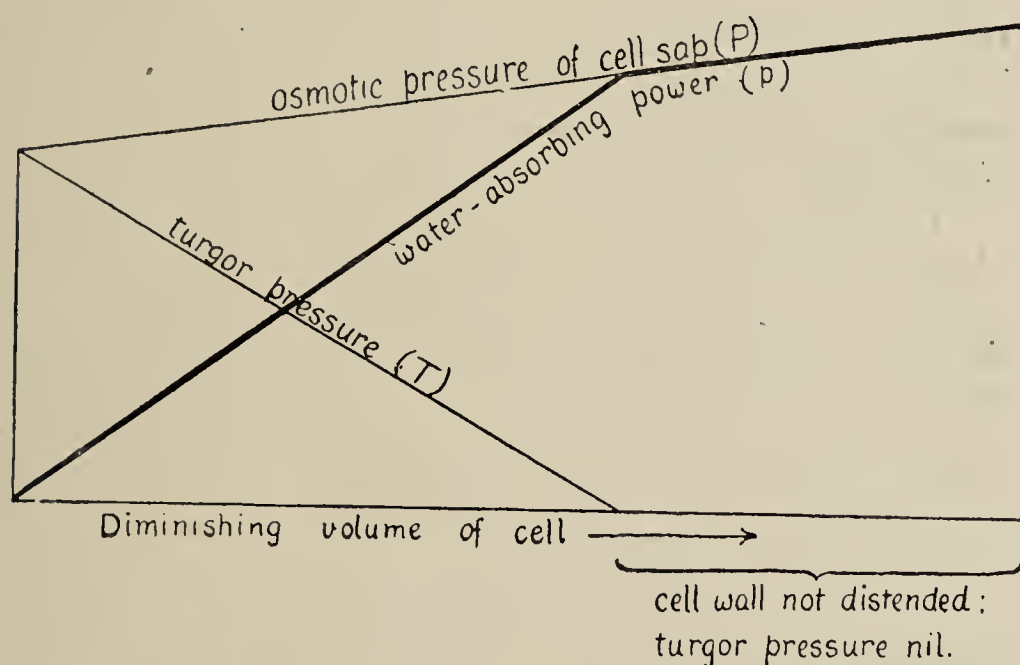
The assumption has been made that, as for most elastic materials, the extension of the cell wall is proportional to the distending force, so that the increase of volume is also approximately proportional to the increment of turgor pressure from the point at which the protoplast begins to distend the wall. As the volume increases (from right to left in the diagram) the concentration of the sap will diminish, and consequently also its osmotic pressure : these changes will be more or less considerable according to the extensibility of the wall.

Applications of the conception of water-absorbing power.

Some important corollaries which are by no means generally realised may now be considered.

(1) *Condition of equilibrium between adjacent cells.* It is evident that the power of one cell to withdraw water from another cell in contact with it does not depend directly or solely upon the osmotic pressure of its sap in relation to that of the other, but upon their relative water-absorbing power. As the condition of

[1] Cf. Renner, Flora, 103, 1911, pp. 239-241.

equilibrium between two cells a and b we have $p_a=p_b$, or $P_a-T_a=P_b-T_b$. If P_a-T_a is greater than P_b-T_b, then cell a will absorb water from cell b, irrespective of the absolute values of P_a and P_b. In fact we may theoretically have cell b with the greater osmotic pressure, yet because its turgor pressure is also greater it may not only be unable to absorb water from cell b but may yield water to it.

(2) *Osmotic pressure and suction force.* It is most important to realise that a *fully turgid cell has no power to absorb water.* It follows from this that the suction force of a transpiring shoot depends on its cells *not being completely turgid,*[1] and increases rapidly from zero as turgor is lost and the "saturation deficit"[2] increases. The suction force of a shoot corresponds to the water absorbing power of its cells, not in general to the osmotic pressure of their sap.

(3) *Automatic regulation of transpiration.* Any consideration of the physics of the generation and transmission of suction force in a transpiring shoot clearly involves the same principle. For simplicity we may imagine a single cell in contact with a vessel. Water is lost by evaporation from the surface of the cell wall, an imbibition force is thus developed and water is withdrawn from the cell sap until the water absorbing power of the compressed proto-plast is sufficient to counterbalance the imbibition force of the wall. The "saturation deficit" necessarily involves a lowering of the vapour pressure at the evaporating surface, and a consequent diminution of the rate of water loss,[3] which will, however, continue so long as this vapour pressure is greater than the tension of water vapour in the air bathing the surface.

At the other end of the cell, water will in the the same way be withdrawn from the cell wall and in turn from the cavity of the vessel.

The condition for static equilibrium is that every component of the system should have the same water absorbing power, or conversely, the same power of resisting the withdrawal of water. The factor corresponding to this in the cavity of the vessel is the tension in the water postulated by the Cohesion Theory. Putting C for this cohesion tension, and I for the imbibition force in the

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[1] " Jede Zelle, die überhaupt transpiriert und saugt, vermag nur infolge eines Sättigungsdefizits zu saugen. Auch in den Blättern normal transpirier-ender, gut mit Wasser versorgter Pflanzen bleibt die Sättigung immer unter dem Maximum." Renner, Flora, 103, 1911, p. 246

[2] Renner's " Sättigungsdefizit," *loc. cit.* On the relation between suction force and saturation deficit, cf. also Livingston and Brown, Bot. Gaz., 53, 1911, p. 311 *et seq.*

[3] It is not suggested that the rate is determined by this factor alone. The behaviour of a colloidal membrane is complicated by other factors, as for instance an increasing resistanse to flow as the water content diminishes.

walls, we have

$$I = p \; [=P-T] = C.$$

The colloidal protoplasm and its various constituents can be regarded not merely as constituting a semipermeable membrane, but also as a separate phase (or phases) capable of developing an imbibition force, or as another osmotic phase separated from the cell sap by the bounding layer of the vacuole, without invalidating the general statement symbolised in the equation.

The same relation also applies to the equilibrium of living cells at all points of the transpiration stream with the water under tension in the vessels. It is not a necessary consequence of the Cohesion Theory that the sap of cells at the top of a tree should be osmotically stronger than the sap of cells lower down. On the other hand the *water absorbing power must be greater at higher levels* as it has to balance a greater tension, due to the greater weight of the longer water column and the added resistance to passage through a greater length of the water channel.

A corresponding relation governs the dynamic equilibrium in a shoot transpiring at a steady rate. At any point in the water stream the rate of flow is directly proportional to the *gradient of water-absorbing power* and inversely proportional to the resistance per unit length, so that for a steady flow we have

$$\frac{p_1 - p_2}{R_{1-2}} = \text{constant}$$

where p_1 and p_2 are the values of the water absorbing power (or, alternatively, the imbibition force or the cohesion tension) at points 1 and 2 respectively, and R_{1-2} is the resistance to flow between these two points.

The writer hopes to deal in subsequent papers with other aspects of the problem of water absorbing power. The structure of the transpiring tissues of xerophilous plants, for instance, requires reconsideration from the mechanical point of view. It is conceivable that in times of drought the water content of the cells may diminish past the point at which the cell walls are completely relaxed. The walls will then be exposed to a tension tending to collapse them and any mechanical resistance they may offer would increase the water absorbing power of the cells over and above the osmotic pressure of their sap. The prevailing cylindrical form of the cells in such tissues, the peculiar ingrowths which characterise the assimilating cells of pines, and the distribution of sclereids in certain leaves are suggestive in this connexion.

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THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.

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Chapter VI.

THE INVOLUCRE.

THE characters of the involucre have been used more or less empirically in various systems of classification, but there appears to have been no critical consideration of the origin and homologies of this structure.

As the involucre is present fully developed in practically all Compositæ it is necessary to consider the evolution of involucral structures in other families where its origin and development can be traced. This is done in Section B of the present chapter which in addition contains a brief account of the history of our knowledge of the involucre in the Compositæ, an analysis of the various types to be found in the family and an indication of the bearing of that variation on the previous phyletic conclusions.

A. HISTORY.

As the involucral bracts are easily observed and show a great variety of form they received a considerable share of the attention of the earlier systematists. Vaillantus (II, 70[1]) used the involucre for his primary divisions of the Cynarocephalæ; Magnol (I, 62) who used the "calyx" as his basis for classification, characterises his "Compositum" as "calice externo includente florem"; Boerhaave (1, 12) gives the involucral characters for each genus; Linné (I, 59) gave a "methodus a calycis" of his own, dividing the "Communes" into eight groups on the character of the involucre. He distinguished various types of involucre such as simple, uniseriate, duplex, calyculate, involucrate, multiseriate with all the bracts similar or imbricate. Berkhey at a later date (I, 9) gave figures of various types of involucral bracts and considered the involucre in some detail, distinguishing the simple, imbricate and calyculate types.

The involucre was used with other parts by Don (I, 25) in his classification of the Cichorieæ, and Gærtner (I, 32), although he did not use this structure for his larger groups, described it carefully for each genus. The involucre is now included in the

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[1] Roman numerals refer to previous bibliographies.

essential characters of all genera, and is also used in the classification of species within various genera, such as *Pteronia* (9), *Centaurea* and *Liabum*.

Cassini (I, 18, Tome I, pp. 255-260) distinguished between the inner involucral bracts, which are usually more or less membraneous, and the outer involucral bracts, which may be very small and rather irregularly arranged or large and closely similar to cauline leaves. He named the collection of inner bracts the "péricline," and the outer bracts when foliaceous the "involucre." Where the outer bracts are small this author considered that a "péricline" accompanied by bracteoles is present. In addition he described the variation in the form of the péricline and involucre at some length, giving the technical terms used in describing the appendages, margins, etc.

Bentham (I, 7) considered this distinction of péricline and involucre to be misleading, and adopted the general term "involucre." This practice has been followed very generally, the difficulty of the cases with foliaceous outer bracts which pass more or less gradually into cauline leaves being met by describing the involucre as duplex. Bentham also discussed the taxonomic value of the involucre, pointing out that this structure may give useful indications of tribal affinities, but must be used with caution on account of its variability even in related genera.

Morphology. Cassini (*loc. cit.*) considered that the members of the péricline were the rudiments of petioles with flowers developed in the axils of all, if uniseriate, or with flowers aborted in the axils of the outer rows, if multiseriate. The members of the "involucre" he homologised with cauline leaves. The leaf base nature of the periclinal bracts is confirmed by Church (3). Bentham (*op. cit.* p. 367) apparently considered all the involucral members homologous with the flower-bearing, inner bracts. The bract-like nature of these inner members is confirmed by various abnormalities, such as that recorded by Offner (IV, 65 and see also descriptions of proliferations by Masters, IV, 52, and Worsdell, IV, 97), and by Church's observations (see Chap. VIII, B). The spines of the anomalous genus, *Xanthium*, were described by Baillon (V, 3) as involucral bracts.

The morphology of the outer involucral members has never been seriously considered, with the exception of Cassini's few remarks, which have been neglected by most synantherologists. Blake (2) and others, however, have noted the similarity of these so-called bracts to reduced cauline leaves.

Biology. The occasional use of the involucre in the wind-dispersal of the whole fruit-head was noted by Hildebrand (V, 30). The protective function and the hygroscopic movements of the bracts are mentioned by Haberlandt (III, 15, p. 552) and Yapp (IV, 98), and form the subjects of short papers by Rathay (12) and Gressner (6). The latter also mentions the hairs which seal the closed involucre in the bud. These had been noted previously by Hildebrand (*loc. cit.*).

Biometrics. As the result of extensive statistical observations Shull (13-14) concluded that the number of involucral bracts shows a seasonal variation due to nutrition differences. The number showed a continuous change, beginning low, increasing for 2-6 days to a maximum and then decreasing for the rest of the flowering period. Shull maintains that the modes of his curves have no connection with the Fibonacci series.

Harris (7) deals with the correlation between the number of involucral bracts and the number of fruits developed.

Mutations. Sudden variations in the involucre are recorded in a few cases, *e.g.*, partial loss of prickles in *Xanthium Woottoni* (IV, 87, pp. 139 and 152), and a peculiar spreading and variation in number of the bracts in *Vernonia rubricaulis* (15). Various abnormalities, chiefly apostasis, are mentioned by Cramer (IV 21) and Masters (IV, 52).

B. Origin and Development of the Involucre.

The capitulum is a racemose inflorescence, usually with a more, or less flattened receptacle on which the florets are crowded. It is frequently considered to be a spike of sessile or nearly sessile flowers with the peduncle shortened. There is, however, another possibility which is usually overlooked—the capitulum may arise by the abortion of the pedicels in a racemose umbel. The two processes are very similar, but in the former the pedicels abort first and then the peduncle, while in the latter the stages are reversed. Although the reduction is similar the products would tend to present certain differences.

In a spike the flowers are usually spaced well apart and the flowers are frequently large. Any reduction in the length of the peduncle would naturally be gradual, and the bracts of the flowers would tend to be reduced by the same causes (decrease in food supply, illumination, etc.), and, therefore, in the same measure as the flowers. The receptacle would rarely, if ever, become flat, and

would tend to be conical and elongated with the subtending bracts of the flowers reduced but still present (cp. Fig. 19, A-B).

In a racemose umbel the flowers are usually already crowded together. The food supply is already reduced, so that the flowers are small, and, as the outer flowers receive more illumination, they tend to become zygomorphic (cp. Goebel, V, 21, p. 552). The pedicels at their insertion on the peduncle are much more crowded than the florets at the top of the umbel, so that the bracts of all except the outer flowers have already become reduced or have disappeared completely. If abortion of the pedicels occurred the florets would then be sessile on a more or less flat receptacle with very reduced bracts to the inner florets or no inner bracts at all. The bracts of the outer florets would form a structure corresponding to the pericline of Cassini (cp. Fig. 19, C-D).
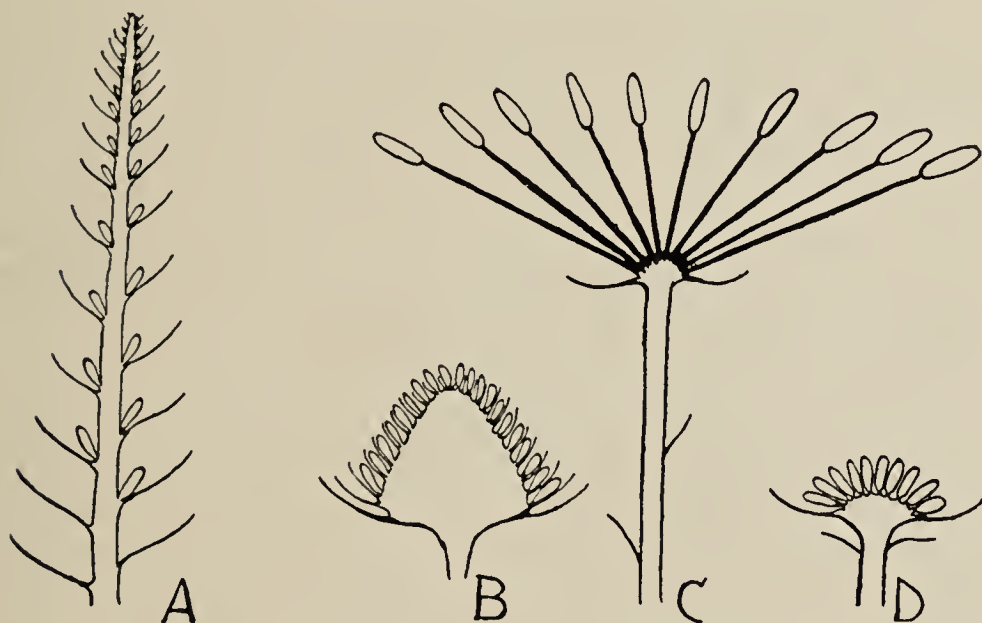
FIG. 19. *Origin of the Capitulum.* A—spike ; B—capitulum derived from spike ; C—racemose umbel ; D—capitulum derived from racemose umbel.

Parkin (10), although he does not discuss the evolution of the involucre at all and makes only a passing reference to the origin of the capitulum, gives a diagram (op. cit. Pl. 18) in which the spike is regarded as a side line and the head as derived from the simple raceme via the corymb and the *umbel*. Masters (IV, 52) records anomalous elongation of the pedicels in *Hypochæris radicata* and *Senecio vulgaris*, etc., by which change " the capitulum assumes the appearance of a simple umbel."

The involucrate inflorescence occurs as a normal form in quite a number of families, *e.g.,* Dipsaceæ, Umbelliferæ, Cornaceæ, Proteaceæ and Eriocaulaceæ, and in many others as an exceptional

type, *e.g.*, *Sphærocoma* in the Caryophyllaceæ (cp. 1, Tab. III), where the involucral bracts are few, small and green ; *Posoqueria densiflora* (Rubiaceæ) where there is practically no receptacle and an indefinite involucre of a few foliage leaves ; and *Monarda* in the Labiatæ (see below).

It may be of interest to note the condition of the involucre in some of these families. In the Monocotyledons *Alisma Plantago* shows cymose umbels with a simple involucre very similar to that of the proliferated *Helenium* observed by Masters (II, 48) ; *Narthecium ossifragum* may be taken as an example of the common phenomenon of progressive crowding in a raceme with bracts and pedicels present, spacing taking place later in the fruiting stage. In the crowded spikes of many orchids bracts are usually present.

Among the Dicotyledons we have the phenomenon of progressive crowding very marked in the Cruciferæ, where the bracts are absent ; this with the corymbose habit gives an approach to the racemose umbel. In the Leguminosæ dense racemes are common ; the pedicels are frequently very short and the bracts much reduced or absent. An involucre is comparatively common in these heads, and may be composed of a few of the outer fertile bracts or 1-2 slightly modified cauline leaves.

In the Araliaceæ (*Hedera* and *Aralia*), the inflorescence is a racemose umbel with the bracts much reduced or absent and no involucre. The Umbelliferæ frequently show the umbel with only the outer bracts forming a uniseriate involucre, but the development of more rows of involucral bracts occurs whenever the inflorescence becomes denser, as in *Sanicula*, where it is uniseriate or indefinitely bi-seriate, and *Astrantia*, where it is bi- or tri-seriate.

The cauline origin of the involucre in *Monarda* is seen clearly in the Labiatæ, where there is a distinct tendency towards shortening of the internodes immediately below the inflorescence. This is well shown in many common Labiatæ, such as *Prunella vulgaris* and *Ajuga reptans*, and a similar phenomenon is seen in *Campanula glomerata*.

In the Campanulaceæ the umbel of *Jasione*, like that of *Astrantia*, has a pluriseriate involucre. The usual tendency in the Lobelioideæ is towards dense spikes with many large foliaceous bracts, but racemose umbels occur also, notably in *Siphocampylus* spp. Below these umbels there are usually a few normal foliage leaves, somewhat crowded on account of the shortening of the internodes as in the Labiatæ.

These few examples serve to illustrate the two sources of the involucre in other families. In the one case the involucral members are the bracts of the outer florets, *e.g.*, Umbelliferæ and some Leguminosæ; in the other case the involucre is composed of purely cauline leaves, *e.g.*, some Leguminosæ, *Anemone*, *Nigella* and *Siphocampylus* spp. The tendency to form secondary aggregations of capitula is present in several families in addition to the Compositæ, and may be illustrated by *Xylia Kerrii* in the Leguminosæ (4).

As the pluriseriate involucre arises either by the progressive sterilisation of successive rows of bracts or by the progressive aggregation of cauline leaves the primitive involucre is obviously the type with a limited number of bracts arranged more or less in one row as in the Umbelliferæ, with or without a small and indefinite number of reduced cauline leaves.

The difference in origin corresponds very closely with Cassini's " péricline " and " involucre "; and the uniseriate periclíne is clearly the primitive type with no sterilisation of bracts, while the " involucre " of a few more or less scattered members is likewise in the primitive condition.

The term " periclíne " will be used here to indicate the leaf-base structures of the involucre which have, or which probably have had, florets in their axils. As the term " calyculus " is in common use it will be used here to denote the outer part of the involucre which originates from purely cauline leaves. This obviates the difficulty of the variation in terminology, duplex involucre, secondary involucre, pseudo-involucre, etc., having been used in various attempts to distinguish between the two parts of the complete involucre (cp. Blake, 2).

Cassini's distinction between reduced and foliaceous members of the calyculus does not seem to be of much importance, when the mobile condition of the vegetative parts, especially in a dense inflorescence, is recognised. The homology of these reduced cauline leaves is obvious in such cases as *Cavea* (IV, 78, Pl.V) where reduction proceeds simultaneously with the progressive aggregation of the cauline leaves, and also in *Gynura elliptica* (8, Pl. 11), *Senecio crepidiformis* and *S. Pearsonii* (11, Figs.8-9). The not infrequent occurrence of apostasis in the calyculus is due to the elongation of nodes which are normally suppressed.

As the complete involucre of the Compositæ usually includes both calyculus and periclíne it seems that both cauline leaves and floral bracts contribute to this part of the capitulum.

The only point now to be determined is whether the capitulum arose from a spike or from a racemose umbel. The smallness and flatness of the receptacle, the very reduced character of the receptacular bracts when they are present, the small size of the individual florets and the dominant tendency to zygomorphy of the outer. florets are all evidence in favour of the origin of the capitulum by the suppression of the pedicels in a racemose umbel.

The only evidence in favour of the origin from a spike is the occurrence of an elongated receptacle together with receptacular bracts in a few of the Heliantheæ, such as *Rudbeckia*, but these are quite advanced in the characters of the style, stamens, corolla and pappus, so that they can scarcely be considered primitive types. This derivation would also leave unexplained the small size of the florets, the dominant tendency to zygomorphy in the outer florets, the reduced condition and frequent absence of the receptacular bracts and, more important still, the dominance of the small, flat or very slightly convex receptacle. All these characters and tendencies are more readily intelligible when the racemose umbel is taken as the ancestral inflorescence.

The view adopted here of the origin and development of the involucre in the Compositæ is briefly as follows: The ancestral racemose umbel by abortion of the pedicels gave a capitulum with the bracts of the outer florets forming a uniseriate pericline, while aggregation of the cauline leaves immediately below the inflorescence gave the calyculus. The primitive involucre has, therefore, an uniseriate pericline with a calyculus composed of a few scattered members. Progressive sterilisation of the floral bracts has given the pluriseriate pericline, while progressive aggregation of the cauline leaves has given a denser, pluriseriate calyculus.

It must be observed, however, that in some cases the calyculus passes gradually into the pericline, but that is a question of phyllotaxis and is considered in Chapter VIII.

C. Analysis of the Involucre in Compositæ.

Taking the uniseriate pericline and the slightly developed calyculus as primitive we can now analyse the distribution of the various types of involucre in the family.

Senecioneæ. The genus *Senecio* again shows the primitive type with a number of variations. The pericline is uniseriate with the bracts free or more or less connate at the base, or there may be a smaller number of " bracts " in a second row. These outer " bracts " are probably a development of the smaller leaves of the

calyculus, which is frequently present. The members of the caly-culus may be few and very small, as in *Senecio vulgaris*, *S. Doria*, etc., but even in these species the number is sometimes as many as eight ; or the calyculus may be multiseriate with the inner members almost equalling the periclinal bracts as in *S. paniculatus ;* or there may be no calyculus. A multiseriate calyculus of 20-40 leaves occurs in *S. lavandulæfolius*: other similar cases are the species of the section *Leptolobi* of Harvey and Sonders.

The involucre in most of the genera of the Senecioninæ is similarly uniseriate, with or without a calyculus ; even in this sub-tribe, however, the involucre rapidly becomes biseriate, as in *Arnica* spp. and *Doronicum*, or triseriate as in *Bartlettia*, or multi-seriate as in *Melalema* and *Culcitium*, or as in *Eriothrix* the involucral bracts may be almost indistinguishable from the densely crowded, reduced leaves of the stem. *Culcitium* is an interesting genus, as it differs from *Senecio* only in the multiseriate involucre, which on larger scale closely resembles that of *S. paniculatus* in the gradual diminution in the size of the outer involucral members. As is usually the case where an artificial distinction is made, the two genera *Senecio* and *Culcitium* pass into each other by inter-mediate species which have been placed sometimes in one genus and sometimes in the other. Indeed, a new genus, *Shafera*, has been founded (5) which differs only in the 3-4-seriate involucre and obtuse style branches, and which is regarded by its author as intermediate between *Senecio* and *Culcitium*. It seems probable, therefore, that the multiseriate involucre in the Senecioninæ is due to a development of the calyculus, the pericline remaining uniseriate.

The Tussilagininæ are usually uniseriate and the Liabinæ multiseriate ; the Othonninæ are uniseriate and are characterised by the greater development of the tendency to connation which is present in *Senecio*.

Cichorieæ. The involucre in this tribe is very varied; frequently the pericline is uniseriate, with a well developed, more or less foliaceous calyculus in one to many rows. The progressive aggrega-tion of the cauline leaves to form the calyculus is occasionally seen in the dandelion. The sub-tribes are again indistinguishable on this character, but the structure of the involucre is closely allied to that of the Senecioninæ.

Calenduleæ. Here the involucre is usually uniseriate with or without a calyculus but is sometimes triseriate in *Osteospermum*, where the calyculus may equal or may be smaller than the pericline.

Arctotideæ. The involucre is multiseriate in all genera except *Landtia* where there are only a few rows of bracts. The calyculus is in a more or less primitive condition in the Arctotidinæ and more developed in the other two sub-tribes.

Anthemideæ. The calyculus is distinct in a number of genera and the pericline uniseriate or biseriate. The number of rows in both pericline and calyculus varies considerably but more or less similarly in the two sub-tribes.

Inuleæ. In the Gnaphaliinæ the Helichryseæ show a larger proportion of genera with the involucre in the primitive condition, *i.e.,* pericline uniseriate, calyculus in one to a few rows. In some genera, such as *Millotia* and *Quinetia*, the involucre closely resembles that of *Senecio.*

A similar condition obtains in the Tarchonanthinæ, one genus having the primitive form and the others a more developed calyculus. In the Filagininæ most genera have only a few bracts, only *Filago* and *Cylindrocline* showing sometimes the multiseriate involucre. The range in the Plucheinæ from a pauciseriate to a multiseriate involucre is covered by *Pluchea,* except the case of *Denekia,* which has a uniseriate pericline and a few similar outer leaves forming the calyculus.

The Athrixiinæ are all multiseriate, while the Relhaniinæ show a large proportion of the genera with the primitive involucre, *Bryomorphe* being similar to *Eriothrix* in that the involucre is practically indistinguishable from the reduced, densely crowded, cauline leaves. A number of the Relhaniinæ have the multiseriate involucre while the Angianthinæ have only two genera, *Cephalip-terum* and *Gnaphalodes,* with the advanced type; all the other genera have either the primitive type or a few, sometimes only two, bracts.

This fact and the difference in the corolla (see Chap. IV) suggests that the Angianthinæ are not so closely related to the other two sub-tribes as is suggested in Fig. 7. They might be better regarded as a special group showing a certain amount of reduction in the involucre, while the Relhaniinæ might be regarded as giving the slightly more advanced Athrixiinæ.

The primitive involucre occurs in a number of the Inulinæ and Buphthalminæ, and the numerous outer rows in the other genera are shown to be a developed calyculus by their frequently foliaceous structure. Indeed, the Inulinæ are as primitive as the Gnaphaliinæ in the involucre.

Cynareæ. The involucre is multiseriate and in the primitive

genus, *Centaurea*, has undergone various modifications; spines or more or less elaborate appendages are frequently present at the apices of the bracts. The pericline is in two or more rows, and usually passes gradually into the calyculus. A similar involucre without the elaborate appendages is the rule in the Cynareæ. The only difference in the sub-tribes is the occurrence of a more or less foliaceous calyculus in two or three genera of the Centaureinæ.

Mutisieæ. In the Barnadesiinæ, Onoseridinæ and Gochnatiinæ the involucre is multiseriate without exception, This is interesting when the involucre of the Nassauviinæ is considered; there only three small genera are multiseriate, the others varying from five or six bracts to a few rows. *Perezia* has two to many rows, the pericline being uniseriate and the calyculus frequently foliaceous. In *Trixis* the pericline is composed of from five to ten bracts in one row, and the calyculus is usually a few leaves, sometimes small, sometimes larger and foliaceous, rarely more numerous and in several rows. This is exactly the condition in *Senecio* (cp. Chap. V, Sect. D). In *Nassauvia*, where the cauline leaves are reduced and crowded they pass very gradually into the calyculus, cp. *Bryomorphe* and *Eriothrix*.

Vernonieæ. The involucre is multiseriate as a rule, reduced to a few bracts in *Corymbium*, *Rolandra* and *Spiracantha*, and pauciseriate in a few other genera. *Vernonia* and two or three other genera of the Vernoniinæ have the calyculus occasionally foliaceous.

Astereæ. The involucre is frequently multiseriate, but in the Homochrominæ an uniseriate pericline with a more or less foliaceous or reduced calyculus occurs in a number of genera and it is the rule in the Bellidinæ and Grangeinæ. This primitive involucre is the commonest form in the Conyzinæ and Baccharidinæ, but in both these tribes it is occasionally multiseriate. The Heterochrominæ is very similar to the Homochrominæ with even a larger proportion of genera showing the primitive involucre. The chief genera, however, are all multiseriate, except *Erigeron* and some species of *Felicia* which are biseriate.

Eupatorieæ. The involucre in Eupatorieæ varies from one to many rows, with the calyculus small or equalling the pericline in the size of the leaves. *Mikania* is distinguished from *Eupatorium* by its pericline of four bracts with or without a few membered calyculus. The other genera vary from uniseriate (*Stevia*) and bi- to triseriate (*Ageratum*) to pauciseriate (*Alomia*). The smaller genera vary within a similar range. In the Piqueriinæ, with the

exception of *Decachæta*, the primitive involucre is the rule. The multiseriate type occurs in the chief genera of the Adenostylinæ, a few others showing the primitive type.

Heliantheæ. The primitive involucre is the rule thoughout the Helianthæ with only a few exceptions. The difference between the pericline and the calyculus is frequently so marked that the involucre is known as duplex, even by those systematists who do not recognise the essential difference between the pericline and the calyculus which is commonly quite foliaceous in this tribe. There is so much similarity in the sub-tribes that it is unnecessary to consider them in detail with the exception of the Madiinæ where the calyculus is sometimes absent, and the Galinsoginæ where the uniseriate pericline and slightly developed calyculus confirm the affinity of that sub-tribe with the Helenieæ.

Helenieæ. Here the pericline is without exception uniseriate and the calyculus is absent or only slightly developed except in the more important genera of the Jaumeinæ.

D. Phylogenetic Significance of the Involucre.

The establishment of a sound view of the morphology of the involucre with a definite primitive type enables us, as with the pappus, to analyse with some clearness the large number of varieties of this part of the capitulum and to obtain some information of phyletic value.

The primitive position of the Senecioneæ and *Senecio*, the passage of. the Senecioninæ into the Vernoniinæ *via* the Liabinæ, the positions as in fig. 7 of the Othonninæ, Tussilagininæ, Cichorieæ, Calenduleæ and Anthemideæ are all confirmed. The Arctotinæ is clearly the primitive sub-tribe in the Arctotideæ.

A slight rearrangement of three of the sub-tribes in the Inuleæ is suggested and corroboration of the position of the others obtained. The Centaureinæ is confirmed as the primitive group of the Cynareæ. *Trixis* as the basal genus (arising from the Senecioneæ) and the Nassauviinæ as the basal sub-tribe of the Mutisieæ have the involucre in the primitive condition.

The positions of the sub-tribes in the Vernonieæ, Astereæ and Eupatorieæ are confirmed.

The relative primitiveness of the Heliantheæ, the derivation of the Helenieæ from the Galinsoginæ and the advanced position of the Jaumeinæ are supported by the evidence of the involucre.

Without exception, therefore, the characters of the involucre in the Compositæ substantiate the phyletic conclusions given in fig.

7, Chap. II and modified in Chaps. III-IV. This, it should be noted, is with the uniseriate pericline and slightly developed calyculus taken as the primitive type of involucre, a view which derives strong reciprocal support from the fact that with this hypothesis the involucre slows an evolution essentially similar to that of the other characters of the capitulum.

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CHAPTER VII.
THE RECEPTACLE.

WE have now reached a stage where it is admissible to use previous phyletic conclusions in the interpretation of the morphology and phyletic value of the remaining structures of the capitulum. As the structure and irritability of the styles and stamens, the structure and colour of the corolla, the structure of the pappus and involucre have all been shown to indicate the same evolutionary lines, the structure of the receptacle should be explained in the light of these facts. This is done in Section B and the usual sections on the history, the distribution of forms within the family and the phyletic value are included in the present chapter.

A. HISTORY.

Like the involucre, the receptacular paleæ are among the more obvious features of the capitulum and as such were used at an early date in the sub-division of the family. Vaillantus (II, 70) distinguished various sub-groups of the Corymbiferæ and the Cichoriaceæ on the basis of the naked, paleaceous or pilose nature of the "placenta." Pontedera (I, 71) distinguished naked, squamate, pappose, and villous types of "thalamus." Gaertner (I, 32) also used the receptacle for his sub-divisions, distinguishing the alveolate form in addition to previously recognised types. Berkhey (I, 9) has a chapter on the receptacle, distinguishing four types of surface and giving numerous figures in Tab. VII.

Cassini (I, 18, Tome I, p. 252) gives a very precise and detailed account of the variation in the receptacle or "clinanthe," distinguishing five parts and eight kinds of appendages, and differentiating between the paleæ with florets in their axils and paleæ which are more numerous than the florets and surround them. Bentham (I, 7, p. 368) gives another account of the variation in the receptacle and points out that the receptacular paleæ are homologous with the involucral bracts; Blake (2) also notes this homology. It applies, however, only to the members of the periclinal part of the involucre (cp. Chap. VI, B). Bentham apparently confused the two kinds of receptacular paleæ in the Buphthalminæ (I, 7, p. 369) but afterwards (I, 8, p. 337) noted the setiferous character in a number of genera in that sub-tribe. He also (*loc. cit.*) criticises Don's use of the receptacle (I, 25) in the classification of the Cichorieæ.

Abnormalities. Cramer (IV, 21) refers to cases of the abnormal development of receptacular paleæ in *Hieracium* and *Pyrethrum*, in which there are normally no paleæ. Goebel (V, 21, p. 397) mentions gradual transitions from involucral bracts to setiform paleæ in *Xeranthemum macrophyllum*, but, as above-

mentioned (Chap. V, A), he maintains that a qualitative change has taken place and that these "bristle-scales" are "bristle-scaies" not paleæ.

Development. Kraus (V, 44) considered that the foveole was epidermal in origin, but Yapp (IV, 98) points out that although the ridge is epidermal, the floor of the foveole has a more deeply seated origin. The late appearance of the ridge of the foveole and its origin from the epidermis is also noted by Martin (II, 47).

Biology. The arching of the receptacle which occurs in *Taraxacum* and other genera, by means of which the stipitate, parachute pappus is accommodated on a more or less hemispherical surface, is noted by Benecke (1) and Kronfeld (3).

B. VARIATION IN THE RECEPTACLE.

Cassini's analysis of the various forms assumed by the receptacle and its appendages is more precise than Bentham's but the terms given by the latter will be used in the following description because they are in more general use.

The receptacle is usually flat or slightly convex, occasionally it is conical and more rarely it is concave. This dominance of the flat or nearly flat receptacle is explained by the suggested origin of the capitulum from a racemose umbel (Chap. VI, B), and it is worth noting that Bentham (I, 7, p. 368) regarded the elongated conical receptacle as a character of no more than specific value.
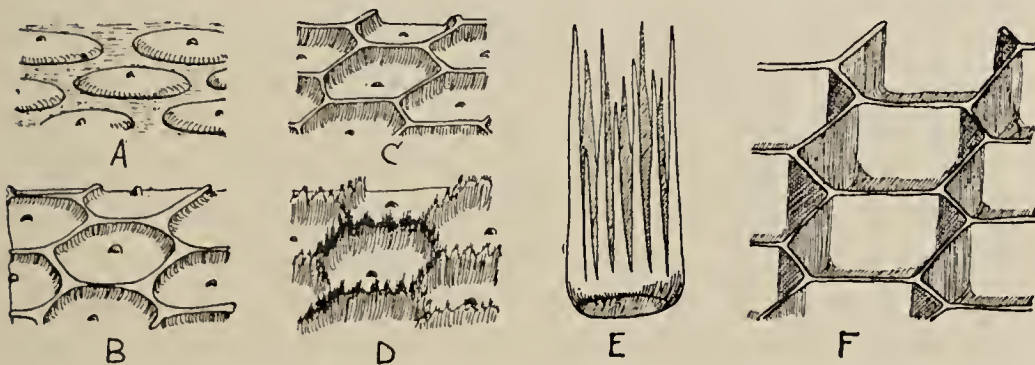
FIG. 20. *Receptacle Forms in the Compositæ.* A—scrobiculate; B—foveolate; C—areolate; D—fimbrillate; E—setiferous (one segment); F—alveolate, shallow alveoles with entire margins.

The surface of the receptacle is described as *scrobiculate* (Fig. 20, A) when it is covered with low mounds of tissue with furrows between, the top of each mound being occupied by the remains of the vascular bundle, which supplied the lower distributive centre (cp. II, 63) ; as *foveolate* (Fig. 20, B) when it is covered with shallow circular or polygonal depressions, each with the above-mentioned small vascular protuberance; as *areolate* (Fig. 20, C) when the depression is polygonal, more or less flat-bottomed and surrounded by a low, narrow ridge ; as *fimbrillate* (Fig. 20, D) when this ridge is higher, with the margin lacerate, denticulate or cut up into a

number of short paleæ; as *setiferous* (Fig. 20, E) if the laciniæ of the margin are long and narrow like the paleaceous setæ of the pappus; as *alveolate* (Fig. 20, F) if the ridge is higher still with the margin entire or variously divided.

In addition to these variations there is the *paleaceous* receptacle with membraneous scales, each of which subtends a floret. The latter point is frequently ignored and the term paleaceous applied to the setiferous receptacle but, as Cassini and Goebel maintain, there is an essential difference between the paleaceous setæ, which surround the achene, and the paleæ, which occur in the positions of bracts.

Considering the origin of the capitulum from the racemose umbel, it is probable that the inner bracts were already very much reduced or entirely absent before the suppression of the pedicels. The appearance of scale bracts or other structures among the sessile florets would in that case be either reversion or a new development. The sporadic appearance of paleæ in the position of bracts in genera or even species with all their relatives non-paleaceous has all the characteristics of atavistic variation. The series of variations from the foveolate to the alveolate and setiferous types shows a progressive development of the ridge between the depressions which clearly constitutes successive stages in the development of secondary structures. Their secondary nature is confirmed by their first appearance after the formation of the gynœcium in the development of the capitulum (see Martin, II, 47, p. 355 and Pl. XIX, Fig. 9b).

The primitive receptacle would, therefore, be flat or nearly so and would show a foveolate structure, with reversion to a pre-Composite ancestor evident in the occasional appearance of paleæ in the positions of bracts, and with the subsequent development of the setiferous and alveolate types indicated by the occasional appearance of the fimbrillate type.

C. Analysis of the Receptacle Forms in the Compositæ.

As pointed out at the beginning of this chapter the evidence from all the other parts of the capitulum is so strongly in favour fo the general scheme of evolution shown in Fig. 7 that the variation in the receptacle must be considered in relation to these other phyletic data.

Senecioneæ. These data clearly indicate the Senecioneæ as the basal sub-tribe and *Senecio* as the basal genus. The condition of the receptacle in that genus is, therefore, very interesting. Bentham (1, 8) describes it as flat or slightly convex, naked, foveolate or shortly

fimbrillate; this is quite in accordance with the conclusion arrived at in Section B, but the atavistic appearance of receptacular paleæ also occurs, *e.g.*, occasionally in *Senecio (Senecillis) glauca*, Gaertn., Fig. 21. This anomaly has not previously been recorded in *Senecio* and adds one more to the numerous cases in this genus of variations which indicate the "critical tendencies" throughout the family, and which taken together leave very little doubt of the correctness of the view that *Senecio* is the basal genus of the Compositæ.

Fig. 21. Sub-biseriate involucre and palcaceous receptacle of *Senecio glauca*, Gærtn.; an abnormality in an authentic herbarium specimen. Magnification—about 3 diameters.

The receptacle in most of the Senecioninæ is flat and naked, but conical receptacles and foveoles occur in a number of genera and the fimbrillate type in some species of at least six genera. *Raillardia* which has been removed on insufficient grounds to the Heliantheæ by Hoffman has the receptacle setiferous; *Bartlettia* is more or less scrobiculate and *Arnica* is often villous. The range in the Senecioninæ is, therefore, that of all the more primitive forms of receptacle.

Fimbrillate alveoles occur in *Euryops* in the Othonninæ but as a rule the receptacle is naked or foveolate both in that sub-tribe and the Tussilagininæ. The range in the Liabinæ is interesting : *Liabum* is naked, alveolate or fimbrillate; *Gougrothamnus* (=Sect. IV of *Vernonia*, Hoffman) is foveolate; *Neurolaena* has caducous paleæ and *Schistocarpha* deciduous paleæ.

Vernonieæ. The same amount of variation is shown by the Vernoniinæ, where the receptacle is usually naked. In *Vernonia* it is naked, foveolate or fimbrillate. Foveoles occur in a few species of only two genera in the Lychnophorinæ, the others having no appendages.

Cichorieæ. All the receptacular forms occur in this tribe and, according to Bentham, have very little taxonomic value ; the paleæ

when they occur are very thin, usually deciduous and not at all like bracts. Bentham (I, 7, p. 482) agrees that the Cichorieæ are probably the most recent tribe, so that the sporadic appearance of paleaceous bracts is strong evidence of their atavistic nature.

Calenduleæ. Practically without exception the receptacle here has no appendages.

Arctotideæ. This tribe has the alveolate type well-developed ; the margin of the alveole may be entire or variously divided. In *Ursinia* the alveole is divided almost or quite to the base so that each achene is surrounded by a number of narrow paleæ, free or fused in a ring at the base. Three small genera show the naked or foveolate types, with, in *Haplocarpha*, a tendency to develop the fimbrillate form. The Gundeliinæ are markedly setiferous, so that the relative positions of the sub-tribes and the primitive position of *Ursinia* are confirmed by the characters of the receptacle.

Anthemideæ. The only distinction, and it is admittedly artificial, between the Anthemidinæ and Chrysanthemidinæ is the presence of receptacular paleæ in the former and their absence in the latter. The latter sub-tribe has, as a rule, no appendages on the receptacle, but foveoles. fimbrillæ, setæ, alveoles and even a few short paleæ occur in some of the genera, so that even this artificial distinction breaks down in a few cases. Reclassification on a natural basis is required.

Inuleæ. The receptacle here has no appendages as a rule, but paleæ occur in a few species in almost every sub-tribe and the other types occur so sporadically that few phyletic data can be obtained. It may be noted, however, that *Helichrysum* is naked, foveolate or alveolate and *Gnaphalium* naked or foveolate, so that the primitive receptacle occurs in the chief genera of the primitive sub-tribe.

The only other point of interest is the predominance of the setiferous type in the Buphthalminæ where every genus shows an approach to this character, some with paleaceous bracts which surround the florets, others with the true setiferous form, cp. Cynareæ below. Bentham's remarks (I, 8, p. 337 sqq.) on two of these genera are of interest, especially as he considered the Inuleæ to have no real affinity with the Cynareæ (see Chap. I, Fig. 2) *Geigeria*, he says, has the receptacle and corolla of the Cynareæ; *Rhanterium* is stated to have the habit of *Centaurea* with the exception of the ray florets.

Cynareæ. The receptacle in all but three genera is setiferous, the setæ being slender, or flat and more or less paleaceous. The exceptions are *Berardia* and *Warionia*, removed to the Mutisieæ by Hoffmann, and *Onopordon* in the Carduinæ, where the receptacle has foveoles or shallow alveoles with the margin more or less lacerate. This is so exceptional in the tribe that it is better regarded

as a reversion, especially as *Onopordon* shows no other primitive characters.

Mutisieæ. The receptacle here is frequently naked or foveolate, paleæ occur in a few small scattered genera. The condition in *Trixis* is of interest (cp. Chap. V), the receptacle is naked or fimbrillate, the fimbrillæ being very slender. This is quite in accordance with the primitive position suggested for that genus. No difference in the condition of the receptacle can be traced as distinguishing the various sub-tribes.

Astereæ. The Homochrominæ and Heterochrominæ show a scattered distribution of all the receptacular forms. The Bellidinæ and practically all the Grangeinæ have no appendages. The Conyzinæ are naked, foveolate or fimbrillate and the setiferous form in addition to these appears in the Baccharidinæ.

Eupatorieæ. The receptacle here is usually naked but is pubescent in a few genera and alveolate in *Hofmeisteria.* Caducous or deciduous paleæ occur occasionally in eight genera, which are mostly small or monotypic.

Heliantheæ. The normal condition of the receptacle in this tribe is paleaceous. The paleæ may be broad and persistent, or narrow and more or less deciduous, subtending the florets : there may be as many scales as there are florets or, as is frequently the case, the scales may be reduced or absent in the centre of the capitulum, or as in many other cases the paleæ may be narrow and more numerous than the florets, surrounding, not subtending, them. As the Heliantheæ are an advanced tribe in practically every other character of the capitulum, it is obvious that the paleaceous receptacle is not the primitive character which it has been assumed to be by Bentham (I, 7, p. 482) and others, but is partly the expression of a tendency to revert to a pre-Composite ancestor (which tendency is present in *Senecio* but attains its highest development in this tribe) and partly the expression of the tendency of the foveoles to develop into the setiferous form.

The return to the normal condition for the family takes place at the end of the Coreopsidinean line in the Milleriinæ where paleæ are seldom present and the receptacle has normally no appendages. The Lagasceinæ also show no appendages. All the other tribes aave paleæ either subtending or surrounding the florets in practically every genus.

Helenieæ. As this is one of the few tribes from which floret-subtending paleæ are completely absent, the relationship of the Galinsoginæ and Tagetinæ requires examination. The receptacle in the latter sub-tribe is usually naked or fimbrillate and is alveolate with lacerate alveole margins in *Adenophyllum.* At least three of

the genera of the former sub-tribe have the paleæ more numerous than the florets and more or less connate in lacerate alveoles. As one of the three is *Calea*, the chief genus of the sub-tribe, corroboration of the previously suggested affinity is obtained when the receptacle is examined in detail. The Heleniæ, therefore, are an end group with no paleæ, corresponding to the non-paleaceous Milleriinæ on the other main evolutionary line of the Helianthæ (cp. Fig. 7). The Jaumeinæ and Flaveriinæ have no receptacular appendages; the Heleniinæ have appendages only in two genera, long setæ in *Gaillardia* and foveoles in some species of *Hymenoxys*. The Baeriinæ are usually naked, but show all the types except the paleaceous receptacle.

D. The Phylogenetic Significance of the Receptacle.

The receptacle, like the pappus and involucre, is of doubtful taxonomic value, but the critical tendencies shown by the primitive tribe again give the clue to the phyletic interpretation of the variations. Taking the alveolate and setiferous types as advanced, the foveolate and naked forms as primitive and the receptacular paleæ when they subtend florets as reversions to a pre-Composite ancestor, the variations shown by the receptacle confirm in one or two points the previous phyletic conclusions, while the rest of the data are not opposed to these conclusions.

The Senecioninæ and *Senecio* are confirmed as basal; the Liabinæ are confirmed as the source of the Vernoniinæ. The evidence is in favour of *Ursinia* being the primitive genus of the Arctotideæ and of the position of the Gundeliinæ as in Fig. 7. In the Inuleæ the primitive position of the Gnaphaliinæ and the Buphthalminæ as the source of the Cynareæ are confirmed.

The need for reclassification of the Cichorieæ and Anthemideæ on a natural basis is again emphasised.

The position of *Trixis* at the base of the Nassauviinæ is strengthened. The position of the Helianthæ above the Senecioneæ, the position of the Milleriinæ and the derivation of the Tagetinæ from the Galinsoginæ are all confirmed.

The receptacle, therefore, although of little taxonomic or phyletic value furnishes evidence in favour of the suggested origin of several tribes, *viz.*, Cynareæ, Helianthæ, Heleniæ, Mutisieæ and Arctotideæ.

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THE vegetative part of the plant in the Compositæ varies so markedly that it is of little use in taxonomy or phylogeny apart from the special vegetative organs of the capitulum which have been considered in Chapters VI and VII. Nevertheless it is of interest to consider the occurrence of opposite and alternate leaves throughout the family, as even this variable character agrees in several points with previous phyletic conclusions; this is done in Section B. In addition the phyllotaxis of the capitulum is of considerable interest and is discussed in Section A of the present chapter. A brief summary of the phyletic data obtained in the study of the phyllotaxis of the family is given in Section C.

A. PHYLLOTAXIS OF THE CAPITULUM.

The variation of the number of the ray florets in the Compositæ, being easily observed, has furnished a basis for much of the work on the significance of the Fibonacci series.

History. For a full account of the salient features in the history of phyllotaxis in general, readers are referred to Church (1, Pt. I). Wydler (29) seems to have been the first to consider phyllotaxis in the Compositæ in any detail and he gives the data for the capitula and leaves of many species. Ludwig (15-18) gives maxima for the ray florets at 5, 8, 13, 21 and others of the Fibonacci series. He used the Schimper-Braun accessory series to explain the secondary and tertiary modes observed (18). A little later Haacke (6) found similar monomodal variation curves, but the modes in many cases did not fall in the Fibonacci series and from his data he concluded that the number of rays florets varied with the locality and the nutrition of the plants. Haacke thus anticipated the modern work on place-constants and seasonal variation.

About the same time Weisse (25) published a long account of the phenomenon, with a good bibliography and a summary of the periodicity theory as given by Ludwig. Weisse also considered the phyllotaxis of the disc florets, describing it in terms of curve systems (cp. Church). He pointed out that the rays come at the ends of the long curves, *e.g.*, a capitulum with a 21 : 34 curve system has 21 rays. He agreed with Haacke in regarding the multimodal curves obtained from uncultivated material as due to nutrition and not to the presence of true races. This same author has also given a brief account (26) of Schwendener's mechanical theory of

phyllotaxis.   Church (1, Pt. I, p. 16) remarks of this theory that
"it superimposes a second doubtful hypothesis on the original
unsatisfactory one of Schimper and Braun." .

Most of the more modern work agrees in finding seasonal and
local changes in the number of ray florets, the modes not being
confined to the Fibonacci series (see VI 13, VI 14 ; 5, 12, 13, 14, 19,
23, 24, 27).   Strickland (22) in one of the most recent notes on the
subject returned to the concentric circles of the Schimper-Braun
hypothesis, but was answered within a month by Henslow (11), who
referred to his own observations on phyllotaxis (7-10).   In spite of
the variation observed, a monomodal curve with the mode at 21 is
very common in the Compositæ (cp. 20, 28).

Church's work.   This author, in addition to various notes (2-4) on
the simpler aspects of phyllotaxis, has published the most complete
exposition of phyllotaxis in general and of the phyllotaxis of the
capitulum in particular (1).   Some of the points explained by Church
which are directly relevant will now be given, but as the phyletic
value in the Compositæ of these very interesting data is rather
restricted readers are referred to the original for details.   Indeed,
for the proper comprehension of what occurs in the capitulum a
close study of Church's monograph is essential and all previous
work may be regarded as more or less superficial when compared
with that author's fundamental exposition of the subject.

Involucre.   The involucral scales, according to Church, show
a "rising phyllotaxis" and the phyllotaxis cannot, here or elsewhere
in the capitulum, be given a real value in the fractional system of
Schimper and Braun.   In dealing with the phyllotaxis of *Helianthus*
(op. cit, Pt. I, p. 25) he says "the vegetative leaves pass gradually
by reduction into an involucre of leaf-base scales."   The study of
the phyllotaxis of the capitulum confirms, therefore, the theory of
the origin of the calyculus from the cauline leaves by suppression of
the internodes (cp. Chap. VI).

In *Helianthus* the difference between the uniseriate pericline
and the multiseriate calyculus is very distinct.   Taking the case
figured (op. cit., Pt. II, Fig. 50), the whole plant shows a rising
phyllotaxis, from the (3 + 5) of the foliage leaves and the (8 + 13)
of the foliage leaves and calyculus to the (21 + 34) of the disc.   The
transition from the (3 + 5) of the lower cauline leaves to the (8 + 13)
of the upper foliage leaves and calyculus occurs below the calyculus
so that the leaves of that part of the capitulum have the same
phyllotaxis as the upper foliage leaves.   The passage of the foliage

leaves into the calyculus is, therefore, gradual. The passage from the (8 + 13) system of the calyculus into the (21 + 34) of the disc occurs in the pericline, the 21 members of which are transitional and subtend the 21 ray florets at the ends of the long spirals.

In the cases mentioned in Chap. VI, B, where the calyculus passes gradually into the pericline the change from the lower to the higher curve system is not accomplished in the minimum number of members as it is in *Helianthus* and the transition begins with the inner members of the calyculus and continues in the outer members of the pericline. The two parts of the involucre in these cases belong to the same curve system and appear, therefore, to pass gradually into each other.
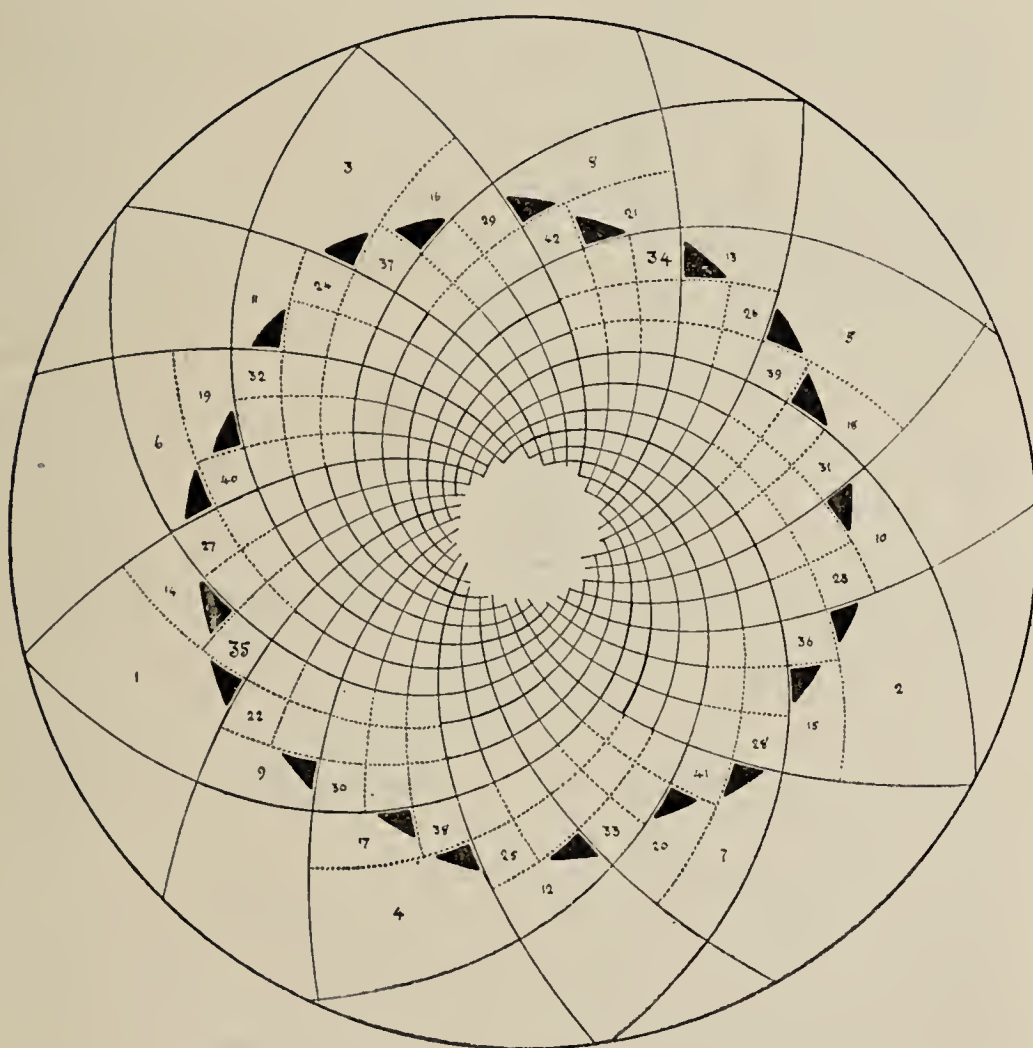
Fig. 22. Expansion system : log. spiral scheme for the introduction of new paths which determine the rise of phyllotaxis ratios in the capitulum of *Helianthus annuus* from (8+13) to (21+34). A small capitulum is taken as a type ; the genetic spiral winds left ; the small amount of unavoidable error in the construction is admitted in the (8+13) system. (Figure and legend after Church.)

Another case is exemplified by *Cynara Scolymus* (op. cit., Pt. II, p. 119) where the distinction between the foliage leaves and

calyculus is very marked, as is the case in most Compositæ. Here there is one transition from the foliage leaves (3+5) to the "outer involucre" (8+13), a second transition from the "outer involucre" to the "inner involucre" (21+34) and a third to the disc florets (55 + 89). The outer and inner parts of the involucre may be considered calyculus and pericline respectively and the transition which occurs to give the calyculus marks off the involucre very definitely from the cauline leaves.

These few examples will be sufficient to show that the morphological distinction drawn between the two parts of the involucre is confirmed by the phyllotaxis.

Ray Florets. Most of the work on the phyllotaxis and biometrics of the capitulum has been done on the ray florets and one of the most interesting points in the whole of the literature of phyllotaxis is the geometrical construction given by Church, which explains the number and position of the rays. The chief points can be seen in Fig. 22,[1]—for the method of construction the reader is referred to the original monograph (1, Pt. II, pp. 116 sqq.). The method consists in adding one long and one short curve to each of the first 13 members of the (8 + 13) cycle and one short curve to the remaining 8 members of the complete cycle.

The ray florets are marked black and it will be seen that they fill in the corners left by the transitional members of the involucre or pericline which are all more oblong than square and thus differ from the quasi-squares of the disc and the outer involucral members or calyculus. The members of the pericline are thus quite definitely indicated and it will be noted that according to this construction the ray florets are always more or less to one side of the subtending bract. This displacement of the floret from the median position is more marked with the outer bracts. It should also be noted that the ray florets occur at the ends of the long spirals, *e.g.*, there are no rays at the ends of the short spirals marked 22, 25, 30, etc. Starting from the bract numbered 1 (Fig. 22) and counting from left to right round the lower part of the circle it will be noticed that the ray florets are grouped thus 2 : 1 : 2 : 1 : 2 : 2 : 1 : 2 : 1 : 2 : 2 : 1 : 2. As there are 21 long spirals there are 21 ray florets, so that the number and position of the rays follows from the geometrical construction adopted.

[1] I am much indebted to Dr. A. H. Church for his kindness in lending me the blocks for Figs. 22 24, which are Figs. 44-46 in the original.

That this is not merely mathematical twisting of facts to suit the construction can be seen from Figs. 23-24. The occurrence of individual capitula with 22 rays involves abnormalities in the system and such a case is shown between the bracts numbered 21 and 34 in Fig. 24 (cp. Fig. 23).
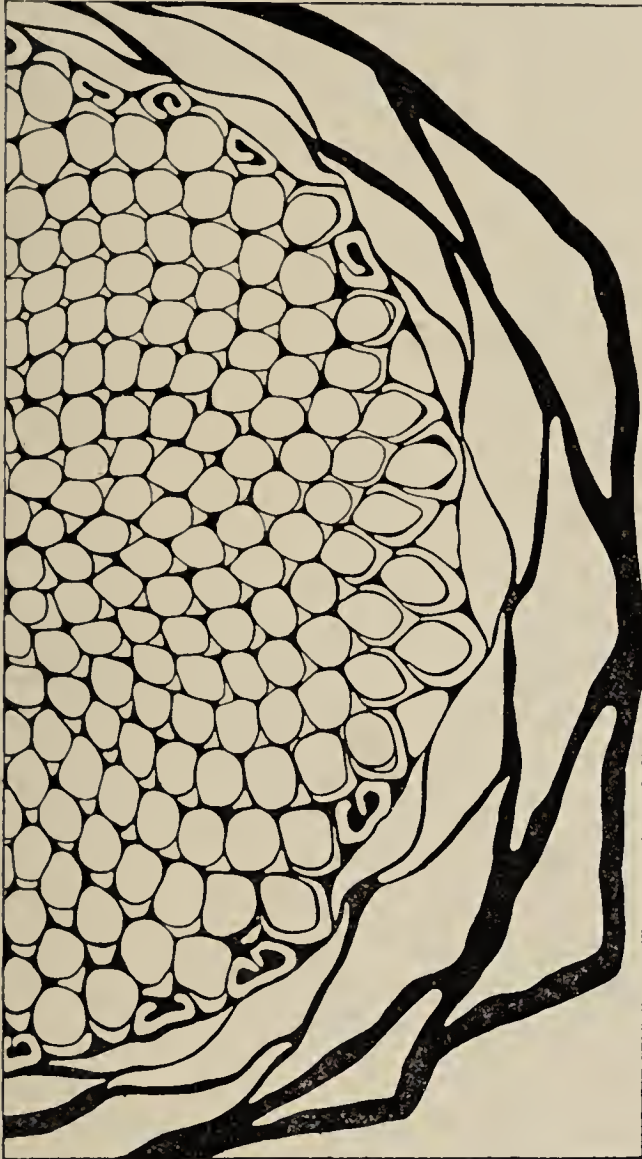
FIG. 23. *Helianthus annuus.* Section of a young capitulum, 10mm. in diameter: cam. lucid. drawing of half the disk. (Figure and legend after Church.)

Similar figures can be drawn for heads with 13, 34 or more rays and are widely different from the artificial figures given by Schwendener and Strickland.

Disc Florets. The theoretical arrangement of the disc florets according to the (21+34) curve system is illustrated in Fig. 22, but, just as rising phyllotaxis characterises the involucre, so falling phyllotaxis characterises the centre of the capitulum. The spirals of the (21+34) system are true to nature up to a point where the size of the floret requires some accommodation in the arrangement. This is necessary because all the florets mature more less simultan-

eously and are of similar dimensions, whereas the space for each floret in the geometrical system grows gradually smaller.

The fall does not appear to take place with the same regularity as the rise, but the Fibonacci ratios occur and mark positions of relative stability in the progress of the fall.   The 21 long spirals continue, but the 34 short spirals become approximately 13 ; these would become the long spirals of the (13 + 21) curve system of the centre.
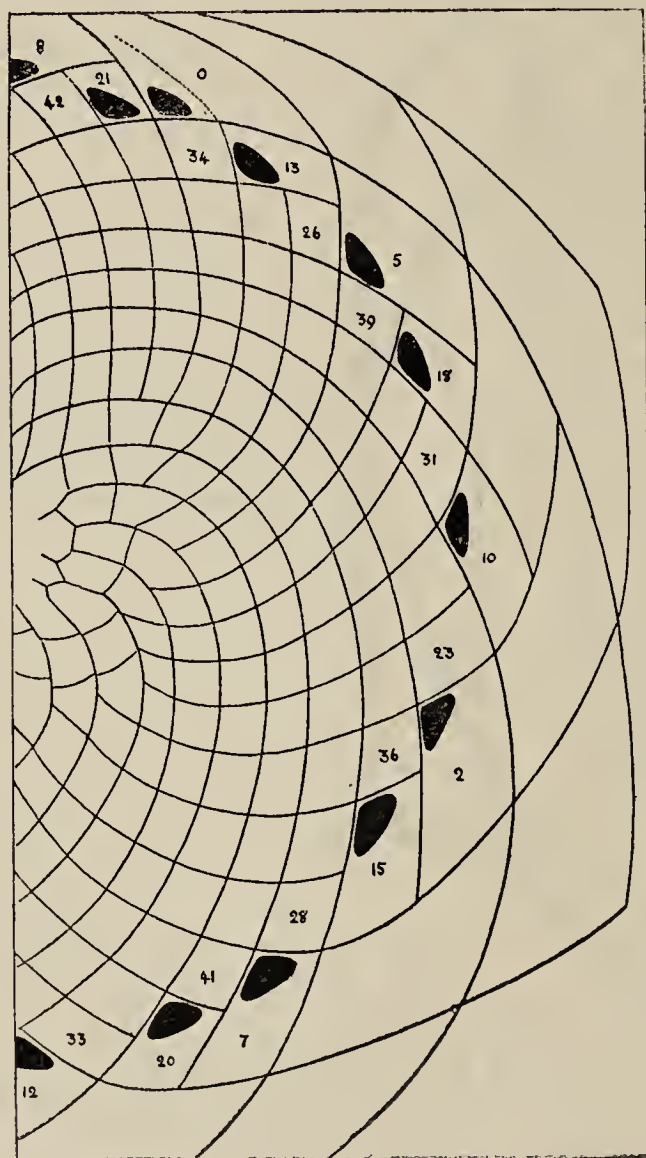
FIG. 24.   Curve-tracing of the preceding: the ray florets are blocked in and the areas   numbered in agreement   with   the theoretical   construction of Fig. 22. (Figure and legend after Church.)

In the upper half of Fig. 24 a tendency to the same 2 : 1 : 2 : 1 : 2 arrangement of the spirals as occurs in the rising phyllotaxis can be seen.   Church gives photographs of capitula in which the falling phyllotaxis of the centre of the disc is more distinct, but observations can be made with most facility on actual fruiting heads of the sunflower and more than one " falling " transition can sometimes be distinguished.

Bijugate Types. In the normal Fibonacci phyllotaxis a single genetic spiral can be traced. This, however, is quite a subjective phenomenon. Other cases occur with two or more genetic spirals and these are described as bijugate or multijugate. Where the capitula are bijugate the phenomenon usually extends to the vegetative parts and the leaves then occur in pairs which may or may not decussate.

This bijugate phyllotaxis is amenable to the same geometrical treatment by means of curve systems of the series $2(5+8)$ or $(10+16)$ etc., (cp. 1, Pt. II, p. 166). Bijugate systems occur rarely in *Helianthus annuus* and are also normal in the terminal capitula of some species, *e.g.*, *Silphium perfoliatum*, where the lateral capitula show the normal Fibonacci phyllotaxis. Other cases in the Compositæ which are sometimes bijugate are *Arnica*, *Spilanthes* and *Zinnia*.

B. Phyllotaxis of the Leaves.

Wydler (29) and Reinecke (21) give numerous data of the phyllotaxis of the vegetative parts of the plant. Cassini (I, 18) confined his attention with very excellent results to the floral characters of the family. Bentham (I, 7) gives a short and not very accurate analysis of the distribution of alternate and opposite leaves in the various tribes.

That opposite leaves are primitive in the Dicotyledons is fairly obvious from the condition of the embryo and is proved by Henslow (8). The addition of one extra member, giving a $(2+3)$ system instead of a $(2+2)$ system is considered by Church to take place very readily, so that an alternate phyllotaxis probably arose at an early stage in the history of the Dicotyledons (cp. Henslow, *loc. cit*).

The fact that opposite leaves are primitive for the Dicotyledons is, therefore, quite irrevelant, and the evidence within the Compositæ is in favour of alternate leaves being the primitive condition for the family. The probable origin of the Compositæ from the Lobelioideæ, where the leaves are practically always alternate, furnishes further evidence.

As the distribution of these two types of phyllotaxis follows the general phyletic lines already laid down, a brief account of the variation will add to the cumulative effect of the evidence for these phylogenetic conclusions.

As before, the Senecioninæ show the primitive type (alternate) with variation showing reversion to the type which doubtless was

primitive in a very distant ancestor. Opposite leaves occur in *Arnica*, *Gynoxys* and *Haploesthes*, which are close relatives of *Senecio*. The Liabinæ have alternate leaves in two genera and opposite leaves in the others. The other genera of the Senecioneæ are all alternate with the exception of *Raillardia* where the phyllotaxis varies.

The Cichorieæ are without exception alternate. The Calen-duleæ are almost all alternate, but *Tripteris* and *Osteospermum* show opposite leaves occasionally. A similar condition occurs in the Arctotideæ, where *Berkheya* and *Didelta* in the Gorteriinæ have opposite leaves in a few species. As the Arctotidinæ are primitive this occurrence of opposite leaves in the Gorteriinæ is one small piece of evidence in favour of that phyllotaxis being atavistic in the Compositæ.

Alternate leaves are the rule in the Anthemideæ but at least six genera, mostly monotypic, are opposite-leaved.

In the Inuleæ opposite leaves occur occasionally or always in one or two genera in each of the sub-tribes, Gnaphaliinæ, Angian-thinæ, Relhaniinæ, Athrixiinæ and there are no exceptions to the alternate phyllotaxis in the other five tribes, including the Buphthal-minæ and Plucheinæ. This fact is of interest as there is also no exception to the alternate phyllotaxis in the Cynareæ, another small point which adds its quota to the evidence for the derivation of the Cynareæ from the Buphthalminæ or Plucheinæ.

The distribution in the Mutisieæ also supports the idea of the opposite phyllotaxis being atavistic. It is absent in the primitive sub-tribe, Nassauviinæ and occurs occasionally in one genus of the sub-tribes, Gerberinæ, Onoseridinæ and Barnadesiinæ and in two genera of the Gochnatiinæ.

The occasional appearance of opposite leaves in the Vernoniinæ, including *Vernonia*, is in accordance with the predominance of that character in the ancestral group, Liabinæ.

At least nine genera of the Eupatorieæ have always alternate leaves; in at least eight others, including *Eupatorium*, the upper leaves are sometimes or always alternate, while the lower leaves are opposite. The other genera, about fifteen, are always opposite-leaved. This condition makes the examination of the Astereæ interesting. There alternate phyllotaxis is the rule with no exceptions in the Conyzinæ and Bellidinæ. In the Homochrominæ opposite leaves occur occasionally in *Pentachæte*, *Lepidophyllum* and in most of the species of *Pteronia* (cp. Hutchinson, VI, 9). In one genus each of the Grangeinæ and Baccharidinæ the leaves are rarely sub-opposite. In the Heterochrominæ the leaves are rarely

opposite in *Olearia,* and the normal condition with opposite lower leaves and alternate upper leaves in *Amellus* is particularly interesting in view of the probable origin of the Eupatorieæ from the Heterochrominæ.

The Heliantheæ although advanced in all their floral characters show atavistic tendencies in the phyllotaxis as well as in the receptacle. Most of the Verbesiinæ show opposite phyllotaxis either entirely or only in the lower leaves. About a dozen small genera are always alternate throughout. Alternate leaves are the rule with a few exceptions in the Ambrosiinæ and Petrobiinæ. Opposite leaves are the rule with a few exceptions in the Lagasceinæ, Zinniinæ, Milleriinæ and Coreopsidinæ. About two-thirds of the Melampodiinæ are opposite, the rest being alternate (cp. the Milleriinæ line in FIG. 7). The Madiinæ are alternate without exception and the condition in the Galinsoginæ is of particular interest. Here, as in the Heleniieæ, about half of the genera show one type and the other half the other type.

The detailed distribution in the Helenieæ is also of interest; the two types occur in almost equal proportions in the Tagetinæ and Baeriinæ; opposite leaves are the rule with one exception in the Flaveriinæ and alternate leaves the rule without exception in the Heleniinæ, cp. FIG. 7.

C. PHYLOGENETIC SIGNIFICANCE OF PHYLLOTAXIS.

The study of the detailed phyllotaxis of the capitulum yields several important phyletic data; the calyculus is proved to be more akin to cauline leaves than to the periclinal bracts; the distinction drawn between these two parts of the involucre in Chap. VI. is upheld; the number and position of the ray florets is proved to be primarily dependent on the bracts of the pericline; the uniseriate type of ray is seen to be the primitive condition in radiate capitula, but the balance of the evidence is still in favour of the discoid capitulum being primitive for the family.

The analysis of the phyllotaxis of the leaves in so far as they are opposite or alternate supplies phyletic evidence which, although of no great value, is of considerable interest in that it follows in some detail the phyletic lines already elucidated.

The most interesting points are noted in Sect. B so that it is only necessary to direct special attention to the phyllotaxis of the Senecioninæ, Liabinæ and Vernonieæ; the Nassauviinæ and the rest of the Mutisieæ; Buphthalminæ and Cynareæ; the Heterochrominæ and Eupatorieæ; the Galinsoginæ and Tagetinæ; and the marked atavistic tendency in the Heliantheæ which is in accordance with the other atavistic tendencies in that tribe.

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THE RECONSTRUCTION OF ELEMENTARY BOTANICAL TEACHING.

EDITORIAL NOTE.

Many teachers have contributed to this discussion, and that is all to the good; but scarcely any students actually attending courses of instruction in botany have sent their views. It is no less important to know in what light the existing teaching appears to the student, and how far it appeals to him as inspiring, satisfying and useful, than to hear the teacher's views as to how far and on what lines it would be desirable to change or modify his teaching. The Editor therefore appeals to any student of botany actually under instruction, who may read these lines, to contribute to the discussion. If anyone prefers to do so under a pseudonym, his confidence will of course be respected.

"THE STUDENT MUST BE GIVEN THE OPPORTUNITY OF HANDLING THE EVIDENCE OF GROWTH AND CHANGE."

To the Editor of THE NEW PHYTOLOGIST.

SIR,

I find myself in hearty agreement with much of the memorandum you have published on the reconstruction of botanical teaching. That there is room for improvement in our university botanical courses will not be denied. The realisation of this has been leading already to a more or less gradual change of balance and emphasis. The discussion you have initiated will, I hope, be followed by a more rapid permeation of botanical teaching with the ideas that govern the more recently fruitful lines of progress, which must be given a larger place than they receive at present. Knowledge of practical value must also be included as far as possible, for if the universities do not disseminate up-to-date information how is it to be disseminated?

Yet with "Witness" and Mr. McLean I would strongly deprecate the relegation of morphology to specialised advanced courses. Even a crude picture of the evolution of plants stimulates the imagination of many students for whom physiology, at least as commonly taught, means little but a dreary waste of formulæ and glass apparatus!

Phylogeny is after all the growth of the race. To follow in imagination the course of creation must ever make an intense appeal. The trouble is that phylogeny has become an *idée fixe*, to the exclusion of other points of view—exclusive, because it has been a narrow phylogeny, based almost solely on the comparison of adult structures. Even phylogeny will be revivified when a synthesis of morphology with physiology (in the widest sense) is effected, and plants are dealt with as the concrete living beings that they are.

Physiology is often anything but the study of plants as living beings, and is justly criticised as suffering at present from a sharp isolation. If physiology were to oust morphology its isolation would be no less.

The teaching of physiology has its own special difficulties. One reason why morphology holds so strong a position is that it is self contained. A student can be introduced to it without any previous knowledge of science; the facts can be directly observed and the processes by which generalisation are reached readily illustrated. Physiology in the more restricted sense demands on the other hand a sound knowledge of mechanics, physics and chemistry, including physical chemistry. Taking facts of structure determined by observation and facts experimentally established regarding nutritive and other metabolic processes of plant life, it seeks to describe them in terms of the physical and chemical principles already available. In the nature of the case this process is enormously complex and difficult. With students who lack a sound preliminary training in chemistry and physics the teacher must provide the necessary knowledge as he proceeds and restrict his field within very narrow limits.

This sort of specialised physiology is not, however, essential to a revivifying of elementary teaching. How the physiological outlook is overshadowed by the traditional morphological bias and, by contrast, how a broader point of view would suffuse greater vitality, can perhaps best be illustrated by a few concrete examples.

In the more elementary practical courses, germination has

been studied mainly from the point of view of external morphology. The functions of cotyledons are pointed out, it is true, and facts like the enlargement of the haustorium in the date seed, for example, which are revealed by a crude morphological examination and are of obvious physiological significance. But how often is attention drawn to the equally striking changes occurring in the wheat grain, where the haustorium does not enlarge? Yet the semi-fluid condition to which the endosperm is reduced is readily observed. It is a simple matter to examine its condition in the later stages microscopically and to apply simple tests, including the test with Fehling's solution for reducing sugars. The facts thus brought home give a good basis for further instruction regarding the digestive processes at work and lend significance to the remarkable semipermeable properties of the grain-coat. Especially for medical students would this aspect of germination have far more interest as well as practical value, than the changes of form, which are more of purely botanical than of general biological interest.

Again, in the study of *Pellia* attention is usually concentrated on the mature form and morphological development of the various organs. But from every point of view one of the most fascinating features is the growth and nutrition of the sporogonium as a parasite upon the thallus. The digestive epithelium of the foot and the distribution of starch are particularly striking. A comparison of different stages reveals further the changes occurring in thallus and sporophyte—the enlargement of the foot, digesting and compressing the tissue below and around it, the hypertrophy of thallus and archegonium and the transfer of starch from the thallus and its accumulation in the seta and capsule.

This example suggests immediately certain practical considerations which are really fundamental. To study *Pellia* in this way means spending more time on *Pellia* in the laboratory. Suitable material must be preserved at the right times of year, and the different stages examined and compared. To bring out satisfactorily the growth changes, drawings must be made to approximately the same scale. In fine, it means a more thorough study of the whole life history and, I am inclined to think, leads inevitably to a modified type system, in the sense that fewer plants must be selected for the practical course, relegating to lectures and demonstrations the presentation of a more general view of the vegetable kingdom.

However this may be, *if life and growth are to become the central facts of our teaching, then the student must be given the opportunity of handling the evidence of growth and change.* He should see not only the winter bud, but side by side with it the expanding twig; not merely the mature storage organ but stages in its formation and sprouting. Flowers should be seen opening, fruits forming and ripening. The secondary growth of a twig should be illustrated by comparable material taken at various stated times of year, so that the student can see the process for himself—can see what kind of wood is formed in spring and in autumn, and can observe the storage and mobilisation of reserves, which is of more importance than the minute histology of the elements.

I am fully alive to the difficulties which confront anyone who attempts to make the necessary changes under existing conditions, with understaffed departments, overcrowded laboratories and unwieldy medical classes. Yet the attempt must be persisted in. Some modification of the first M.B. courses is a particularly urgent matter of policy in face of the movement to cut botany out of the medical curriculum altogether. The principles of general biology should be the central theme; in the selection of material and illustrations utility should be considered; and, as in all university courses, the treatment should be such as to introduce the student to scientific method, train him to observe accurately, honestly and independently, and to draw sound conclusions.

Thus a large place must obviously be given to the elementary general physiology of plant life, including reproduction, heredity and variation, and the influence of environment on form and behaviour; and enough structure and external morphology must be included to illustrate correlation with function and the laws of growth.

Utility demands that attention be given to plant products of immediate importance to human health. One may mention for consideration the food reserves in seeds, fruits, and other food products; the distribution of vitamines; malting of barley, and alcoholic fermentation; nature and properties of vegetable fibres; important bacterial processes; as well as the principles of plant pathology.

As regards method of treatment, although I realise that with large classes the practical course must be to a great extent merely illustrative, I feel strongly that the work most not wholly consist of

looking for things that have already been described in lectures or instructions. Such work gives the opportunity for exercising critical independence where the capacity is already developed, but does little to train those who are not naturally of an inquiring turn of mind. For the average student this end could be served by requiring him occasionally to obtain answers to simple problems, clearly formulated, and soluble with technique easily within his powers. Similar exercises should form an essential (and well advertised) part of the practical examination.

Ideally the laboratory course would not be an appendage of the lectures, but would provide a basis of observed facts on which the lecturer could build. The more this ideal can be realised, the greater will the educational value of our courses become. With students in whom the ever present dread of examinations will not allow the sparks of interest to be fanned into flames, it is so easy for the demonstrator to follow the line of least resistance and spoonfeed, instead of helping them over practical difficulties to the independent observation of facts, the adequate recording of them, and the drawing of sound conclusions. We must persist in the endeavour to remove the incubus, by changing the character of the examinations themselves, or diminishing their relative importance ; and to stimulate interest in the subject for its own sake, not forgetting that the selection of knowledge with an obvious bearing on practical life will succeed with some to whom theoretical principles may not at first appeal.

I am, Sir,

Yours, etc.,

D. THODAY.

ADVISORY COUNCILS—AND OTHER THINGS.

To the Editor of the New Phytologist.

Sir,

Much of your article on botanical teaching in the December issue will be very welcome to those who have for many years attempted to carry out its main thesis, and who have only been prevented from doing so more fully by practical difficulties, *e.g.*, expense, and the necessity of " covering the syllabus." This leads at once to my first practical suggestion :—

(1)   That national advisory councils should be formed of those University teachers (irrespective of status) who are actually doing

the work in question, *i.e.*, biochemistry, elementary botany, etc., whose function it would be to make recommendations to those who draw up syllabuses, and appoint examiners in the corresponding subjects. This would be a more satisfactory way of bridging the existing gulf between teaching and examining than the system of " internal " examinations with "external " examiners—a condition of affairs subject to abuse, and which may be reduced to a farce.

(2) No laboratory should be considered efficient, or recognised by a University, which does not possess a garden and a greenhouse, and, if possible, an experimental station. It has long seemed to me anomalous that in any institution supposed to be for the study of plants, work on the living plant is next to, and in most cases quite impossible! All that is offered, alike to the research worker and the elementary student, is a profusion of the dead bodies of plants, and these usually cut up into inch pieces, with more or less distorted structure. Ecology cannot adequately be taught without frequent excursions, and if possible periodic visits to an experimental station. Could not the Government be petitioned to recognise the great importance of science teaching by granting free travel for genuine ecological work? Field work should not be regarded as a sort of extra, nor the poorly paid assistants expected not only to give over-time work, but to pay their own expenses.

(3) Research on the lines of " the study of plants as living organisms " should be encouraged, since in the long run research is the pioneer of teaching. At present work of this kind simply does not pay; results are far more quickly achieved by rushing material through the microtome, and drawing a few of the sections with an Abbé Camera, and moreover are far less costly in time and money, to say nothing of brain power. More stress might well be laid on the quality as well as the quantity of research produced.

(4) Following from this, and certainly not least in any scheme of reform comes the question of the personality of the teacher. You say that some critics " attribute the lack of vitality and originality to the poor mental quality of the students." This is somewhat naïve, since it is quite possible for the students to attribute the same lack to the poor mental quality of the lecturers! Truly " morphological botany in the hands of a teacher of person-ality and vigour can be made interesting and a real instrument of education," but can those desirable results be achieved in any subject under any scheme by teachers not endowed with those qualities? A botanist known to all your readers once said to me,

"Of course we know that the best people are not in the best posts." Why is this? Is it not because there is no honest effort to secure for the students lecturers of real inspirational power, but rather to appoint those with little or no qualification, but who are "nice people" and "easy to get on with?"

Finally, while in general agreement with your article, and thanking you for the service you have rendered the Science by its publication, and the opportunity thus afforded for discussion, I would protest against the idea that the main function of a University is to provide teaching "with an outlet on practical life." There will always be a large majority who will look after the practical application of knowledge, but let us hope that some may always be found to believe with Miss Sargant that "the great inheritance of the Universities is the tradition of learning for learning's sake."

<div style="text-align:center">

Yours truly,

T. L. PRANKERD

(Lecturer in Botany, University College, Reading).

</div>

April 16th, 1918.

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"NARROW SPECIALISATION DURING THE UNDERGRADUATE YEARS."

To the Editor of The New Phytologist.

</div>

Dear Sir,

May I put forward a few points in connection with the question of the reconstruction of elementary botanical teaching?

Other students with whom I am acquainted agree with me in feeling that there is too much morphology included in the present system. Many students at the beginning of their college life do not clearly know what their future career is to be. An elementary course should present to them all branches of their subject so that they may see what possibilities it possesses for future work either of the nature of research or of a more immediately practical kind. If only one side of their subject is presented to them and they find this dull and unpromising, they may never realise that there are other interesting sides and so may drop the subject as of no use to them.

Students certainly are bored by an excess of morphological detail. I have found that those, especially, who are working for a

pass degree in the University of London are often disappointed on reaching their second (post-Intermediate) year to find how almost entirely morphological their work is likely to be. Subjects such as Ecology or Variation and Heredity which always possess a great fascination for those beginning of the study of biology are hardly dealt with at all.

Under the present system of examinations a parrot-like learning of strings of morphological facts is necessary—the more time that is devoted to this task, the better the examination results. This allows little time for general reading, and the mind is stultified instead of being widened. (By " general reading " I do not mean only that directly in connection with the subject.) There seems to me to be much too great a tendency to narrow specialisation during the undergraduate years, and this is surely the result of the examination system.

What Professor McLean states about students preferring morphological and systematic Botany to physiological is certainly not the case among the majority of students that I know—they usually have a decided leaning towards physiology, a field where there is still much to be discovered, and which exercises the reasoning powers in a way which gives the same sort of pleasure to the mind as geometrical problems. Physiology is not, or should not be, an abstract subject, even though the exact physics of it are in many cases not yet worked out.

Serious students of science should beware of the " sensuous impressions," " mysterious speculations " and " semi-religious fascinations " mentioned by Professor McLean. They are not science, they are not conducive to open-minded scientific enquiry, and they certainly should be eliminated from a course of elementary botany.

Yours, etc.,

June, 1918.   A STUDENT.

THE CLASSIFICATION OF SOME COLONIAL CHLAMYDOMONADS.[1]

By W. Bernard Crow, B.Sc., F.L.S.

[With Two Figures in the Text]

THE Isokontæ show at least three distinct types of plant structure, the filamentous, the cœnocytic and the unicellular. The unicellular forms may be regarded as belonging to one order [21] although a few are best excluded in view of their probable origin by reduction from filamentous forms. This unicellular group is spoken of as the Protococcoideæ [1, 19] or Protococcales [21], names which should be abandoned however because the generic name *Protococcus* has been used to denote a heterogeneous collection of Algæ, and is now used [21, p. 191] to designate forms (=*Pleurococcus*) which are probably reduced members of the Ulotrichales. The name Volvocales is also unsuitable, since *Volvox* is not a typical representative of the group, and the term is in general use to indicate the motile members [14, 15, etc.]. On the whole the general characters are better expressed by the designation Chlamydomonadales, for the whole morphology of the group can be described in reference to that of *Chlamydomonas*. We are here only concerned with the normally motile members, which were formerly subdivided into (a) solitary (b) colonial forms [1, 2, 3, 6, 19], groups which are now known to represent different types of organisation rather than distinct lines of evolution. Some attempt has been made to arrange the genera in more natural families [14, 15]. Amongst the latter most authorities now admit the Sphærellaceæ to be distinct from the Chlamydomonadaceæ, although a closely related line of ascent [4, 15, 17, 21, 22]. The following are the general tendencies of structure :—

SPHÆRELLACEÆ.	CHLAMYDOMONADACEÆ.
Envelope a thick coat, consisting of a thin outer membranous layer and a thick inner gelatinous layer.	*Envelope* a coat of variable thickness, membranous to gelatinous, usually not differentiated.
Protoplasmic outgrowths traversing pits in the membrane.	*Protoplasmic outgrowths* absent.

[1] From the Botanical Department, East London College, University of London.

Contractile vacuoles often more than two, sometimes very numerous, distributed over the periphery of the cell.	*Contractile vacuoles* usually two, in anterior position.
Chloroplast an indefinite parietal sheet or net, often with numerous pyrenoids.	*Choloroplast* a basin - shaped structure, often with few pyrenoids.

Turning to the motile colonial genera of the Chlamydomonadales it is apparent that the cœnobia of *Gonium, Pandorina, Eudorina* and *Volvox* are all of the same type. The three latter genera pass through a plakea stage in their development during which they resemble colonies of *Gonium*. However, it has been shown by Harper [10] that the plate-like form of such colonies can be explained on purely physical grounds. No doubt the evagination of the plakea is also due to mechanical factors. In any case the phenomena of development cannot be used safely for classificatory purposes since Powers [16] has shown that in *Volvox Weismanniana* many of the colonies are turned inside out, so that the originally inner surface comes to lie outside, whilst in others of the same species this is not the case. Finally the resemblance in general type of these cœnobia is not indicative of affinity, for similar colonies are by no means rare in other algæ and Protozoa, whilst the blastula of the Metazoa is planned on the same lines.

One of the characteristic features of *Volvox* is that the power of reproduction is limited to a few cells in the posterior region of the cœnobium, whereas, in the three genera mentioned above, all the cells participate in this process. The connecting link is supposed to be found in species of the so-called *Pleodorina* [see 5, 11] where half the cells are vegetative (*P. californica*), or there is merely a group of four sterile cells (*P. illinoisensis*). The latter form has been shown to be a variety of *Eudorina elegans* [8, etc.] there being all transitions between the typical forms of the latter and the original *P. illinoisensis*.

In material from, an unknown locality[1] I have observed variations in *Pandorina morum* bearing the same relation to the typical forms of that species as *Pleodorina illinoisensis* bears to *Eudorina elegans*, except that the shape and size of the colony are not affected. In one sample some forty colonies in the reproductive condition were examined. Only fifty were absolutely normal

[1] Obtained from Messrs. Flatters and Garnett, Manchester.

specimens of *Pandorina*; in all these the cells of the cœnobium were very rich in food reserves, and in some cases were under-going division. In all the others from one to four cells, usually grouped near one end, were very poor in food material, and were generally much smaller than the rest [Fig. 1]. In a few of the colonies the latter were undergoing division, whilst the few small

FIG. 1. Colony of *Pandorina morum* with one sterile cell, S (reproductive cell, T).

and hyaline cells were very contracted and may have been disin-tegrating. It is commonly found that division of the cells in *Pandorina* is not simultaneous; the case in which some of cells fail to divide at all are only extremes types, probably developed in relation to a restricted nutritive supply.

The differentiation of vegetative and reproductive cells in *Volvox*, then, only represents a fulfilment of the general tendency towards division of labour. A parallel segregation of vegetative and reproductive cells has taken place in many groups of filamentous algæ. Finally it is well known that heterogamy is the result of the same general trend of evolution in nearly all living groups.

It will be seen, then, that we must turn to the cell structure in any attempt to classify the colonial Chlamydomonads. With the the exception of *Volvox* all the latter have a simple gelatinous cell wall, usually distinct from the common mucilage of the colony, but never showing a differentiated outer lumella as in *Volvox* [9, 13, 20] and never with any protoplasmic strings traversing it. Hence these genera have the type of cell wall seen in the Chlamydomonadaceæ.

The other cytological features, too, show that they belong to this family. There is a perfectly typical anterior pair of contractile vacuoles [14], Further their chromatophore can always be traced to the basin-shaped type. *Gonium* is recorded [13] as having this kind of chromatophore, close investigation showing it to be made up of separate granules just as in *Chlamydomonas* (*Chloromonas*) *alpina* Wille and *C.* (*Chloromonas*) *aalesundensis* Wille. The beginnings of this type are seen in *C. stellata* [7]. *Pandorina* and *Eudorina* have a bell-shaped chromatophore [20], the intimate structure of which probably resembles that found in *Gonium* [13]. Merton found a reticulate chromatophore in *Pleodorina illinoisensis* [11], but that this is not necessarily derived from the *Sphærella* type is shown by the evolution of a lacunate chromatophore in *Chlamydomonas* (*Chloromonas*) *reticulata.* The latter is obviously related to *Chl. longistigma* where the beginnings of lacunations are visible on the inner contour of the cup [7]. Grove describes the chromatophore of *Pleodorina illinoisensis* as cup-shaped [9], so there is probably some variability in its form.

The Chlamydomonadaceæ are, as we have seen above, generally characterised by the possession of a pair of contractile vacuoles situated at the base of the flagella, near the anterior pole of the cell. It is true that exceptional species are met with. In *Chlamydomonas pertyi* there are numerous contractile vacuoles, but even here they are found in the usual anterior position. In *Agloë* there are more than two contractile vacuoles, which is merely due to the fact that besides the usual pair there are three accessory vacuoles [15]. Only *Chlorogonium* has its numerous contractile vacuoles distributed over the periphery of the cell, and, as noticed by West [21], this genus is probably more closely allied to the Sphærellaceae than the typical Chlamydomonadaceæ, agreeing with the former in all structural details except in the possession of the differentiated cell-wall with its protoplasmic threads. In fact the vegetative cell of *Chlorogonium* bears a close resemblance to the gamette of *Sphærella.* *Volvox* shows a variation in the number of contractile vacuoles. This is, in itself, an important feature. Of the species investigated *V. globator* has two to six, usually four, and *V. aureus* two, in each cell. Moreover, the contractile vacuoles of *V. globator* are found in a peripheral layer of the cytoplasm, in fact sometimes two of them and often one of them are met with in one of the protoplasmie threads which connect adjacent cells of the colony [12]. The

orientation of these two contractile vacuoles, and the fact they often exceed the two in number certainly points to an affinity with *Sphærella* rather than with *Chlamydomonas*. It may be noted that even in the former genus there is a reduction in the vacuole system, for *Sphærella Butschlii* only possesses two or at the most three [22].

A single chromatophore is found in each cell of *Volvox*. It has the form of a peripheral sheet, comparable with that found in *Chlorogonium*. Young cells of *Sphærella* also exhibit this structure, although at a later stage in their development their chromatophore frequently becomes lacunated and forms a network. The chromatophore of *Volvox* is characterised by its angular outline; it may be protruded deep into the protoplasmic strands which run out rom the protoplast. The same irregular outline is seen in the chromatophore of *Sphærella*, and in *S. droebakensis* the normal zoospore has a continuous peripheral chromatophore protrusions of which run deeply into the pseudopodial outgrowths [22]. The pyrenoid is too variable throughout the Chlamydomonadales to be of any great systematic importance.

The cell-wall of *Volvox* gives this genus its chief claim to be ranked apart from the other colonial Chlamydomonads. Each cell possesses an individual envelope of two layers, a thin outer lamella and a thick highly refractive and mucilaginous inner layer which often renders the wall very massive in proportion to the protoplast. The species of *Volvox* differ somewhat amongst themselves in the form of their separating lamellæ. In *V. tertius* [Fig. 2 C] the globular cells are completely surrounded by the outer lamella, adjacent ones being in contact at their equatorial regions, but otherwise separated by an intercellular jelly. During development [12] the products of division of the mother cell are at first only separated by particularly refractive protoplasmic layers. As soon as division is complete and flagella have been formed the cells separate from one another and a membrane which at an early stage appears as two layers, is seen between them. The mucilage layer is at first relatively thin; it grows much more rapidly than the other parts however, becoming a thick investment. The cells of *V. tertius* thus have fundamentally the same structure as in *Sphærella*. The other species of *Volvox* are slightly modified but possess the same essentials. In *V. globator* [Fig. 2 D] the lateral lamellæ of the hexagonal prismatic cells are common to adjacent elements. In *V. aureus* [Fig. 2 E] the lamella of each cell is

represented by a polygonal hood opening to the interior of the sphere and covering each protoplast, adjacent hoods fitting together and having soft fibrids running from their corners to the middle of the colony where a complete inner lamella of the sphere, corresponding to the aggregated inner parts of the lamella in *V. globator* is formed.
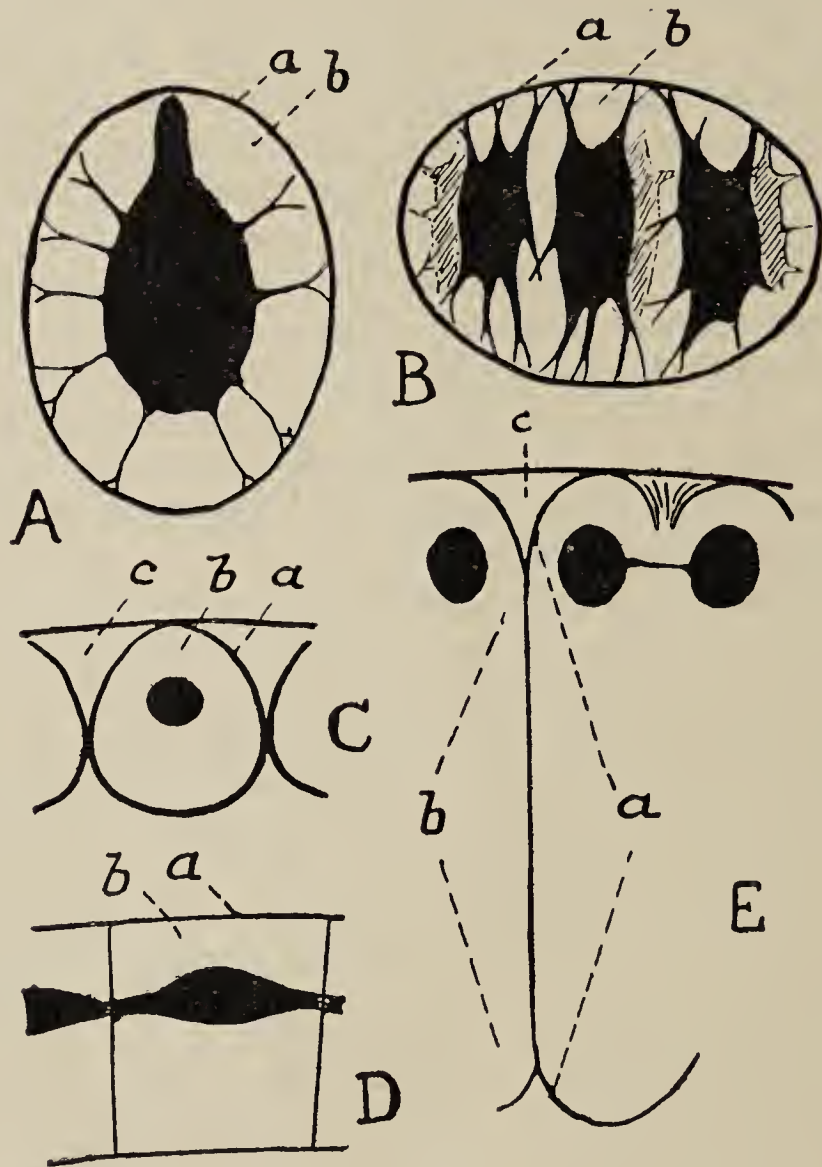
FIG. 2. Diagram to show membrane structure in (A) *Sphærella droebakensis*, (B) *Stephanosphæra pluvialis*, (C) *Volvox tertius*, (D) *V. globator*, (E) *V. aureus*. C, D and E are portions of the outside of the colony in vertical section : *a*, outer layer of membrane; *b*, inner layer; *c*, intercellular mucilage. Protoplasts black.

Still more important than the lamella are the pit-canals in the cell-walls of *Volvox*. They are quite like those of the higher plants and contain strings of ordinary cytoplasm connecting adjacent cells. In *V. globator* they are comparatively wide structures which break up into finer threads in passing through

the lamella. In *V. aureus* they are narrower and pass through in
their entirety. *V. tertius* only shows plasma connections in the
young unborn cells, where they resemble those of *V. aureus*, but
by the time the colony becomes free these strings are no longer
visible. Thus in three closely related species of *Volvox* we have
three very divergent types of plasma-connection. Hence only the
fundamental nature of these structures can be taken into account
in estimating affinities; their actual form is too variable to be
considered. It appears, then, that they are truly comparable with
the outgrowths of the protoplast in *Sphærella*. No doubt they have
taken on a connecting function in relation to the colonial mode of
life of the *Volvox* cells; and it is easy to see how this might have
occurred. Even in the species of *Sphærella* the outgrowths exhibit
the variations that have been enumerated above for the species of
Volvox. Thus in *S. droebakensis* they are wide, show branching
and just beneath the outer skin of the membrane they may divide
up into numerous fine threads [22]. The other species show fine
straight protoplasmic processes.

From the above facts it seems that *Volvox* possesses all the
characteristic features of the Sphærellaceæ, although very distinct
in its colony-form and sexual organs. The genus *Volvox*, has, no
doubt, been evolved independently of the genus *Sphærella* itself,
but on the other hand the similarity between the colonies of *Volvox*
and those of the other colonial Chlamydomonads is really quite
superficial. The family Sphærellaceæ was founded on two genera
Sphærella and *Stephanosphæra*. The latter is a colonial type and
although essentially similar in its protoplast shows quite a
different type of colony organisation, in which at first sight the
cell-wall structure is very different from that of *Volvox*. A com-
parison of the two genera with *Sphærella*, however, accounts for
this. It seems that the colony envelope of *Stephanosphæra* is
homologous with that of the individual cell of *Sphærella* [Fig. 2 B].
Schmidle has pointed out that the only difference between
Stephanosphæra and *Sphærella* is that the former normally has
several protoplasts within the membrane, the latter only one [17].
Sometimes a membrane of *Stephanosphæra* may contain only one
protoplast in which case the organism is indistinguishable from
Sphærella [17]. In *Volvox*, of course, each protoplast has its
own envelope, the whole of these investments fitting together,
sometimes with intercellular mucilege, to form a sphere [Fig. 2 C,
D & E].

Certainly then *Volvox, Sphærella* and *Stephanosphæra* represent one distinct type which stands out among the Chlamydomonadales. There is scarcely more reason for separating this line of affinity as a distinct family than there is for separating other small groups of genera which have arisen from *Chlamydomonas*, and which can in some cases be traced amongst the species of this genus itself [see 7]. In chloroplast structure the Sphærellaceæ appear to be related to *Chlamydomonas* through the forms known as *Chlorogonium*. In cell-wall structure the link is afforded by species of *Chlamydomonas* itself. Fritsch and Takeda [8] have described a species, *C. sphagnicola* which possesses a cell-wall of two layers, a thicker gelatinous inner investment and a thinner firm outer skin. They think the same difference probably exists in *C. glœocystiformis* Dill, whilst in *C. angulosa* Dill the inner gelatinous coat sometimes appears. Finally in *Carteria Fritschi* Takeda there is often a very well developed inner gelatinous layer. Thus the phylogeny of the little group of organisms included under the name of Sphærellaceæ is by no means obscure. It is almost certain that a careful study of the order Chlamydomonadales would reveal other lines of evolution no less interesting.

Summary.

Gonium, Pandorina and *Eudorina* are colonial members of the true Chlamydomonadaceæ.

Reproductive colonies of *Pandorina* possessing one to four sterile cells have been observed.

The genus *Volvox* has arisen independently of the other known colonial Chlamydomonadales; its systematic position is with the Sphærellaceæ rather than with the Chlamydomonadaceæ as at present constituted.

In conclusion I wish to thank Prof. Fritsch for helpful criticism.

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URONEMA ELONGATUM,

A NEW FRESHWATER MEMBER OF THE ULOTRICHACEÆ.

By William J. Hodgetts, B.Sc.

[With Eleven Figures in the Text].

THIS filamentous alga was originally found in February, 1918, in a small pond near Staplehall Farm, King's Norton, Birmingham. It remained rather common until April, being always epiphytic either on a large *Oedogonium* sp., the leaves of *Myriophyllum*, or *Lemna minor* roots, and mixed with various filamentous forms (*e.g.*, sterile *Mougeotia* spp., *Oedogonium* spp., *Spirogyra tenuissima*, *Ulothrix subconstricta* West, etc.) which were fairly abundant amongst submerged grass-leaves, etc., on one side of the pond which was shallow and marshy. Possibly owing to a contamination of the water in the early part of the spring—which probably accounted for the great dominance of *Euglena sanguinea* Ehr. in the pond during the middle of May—the *Uronema*, and also the other filamentous algæ, decreased greatly in abundance and became rather rare towards the end of April and in May. Since the alga differs in many respects from both *Uronema confervicolum* Lagerh. and *Uronema (?) simplicissimum* (Reinsch) Lagerh., the only species

of this genus hitherto described, it has been looked upon as a new species.

The filaments are quite unbranched, attaining a length upwards of 5 mm., and are usually fairly straight, and intertwined amongst other filamentous algæ. The cells are cylindrical, with the exception of the basal cell which is gradually attenuated (Fig. 2), and the apical cell, the tip of which is acuminate, and usually slightly swollen and curved, but never prolonged into a hair (Figs. 1, 3, 4, 5). The possession of an acuminate apical cell is the chief feature which distinguishes the genus *Uronema* Lagerh. from *Ulothrix*, although the mode of attachment also appears to be different in the two genera, the filaments of *Uronema* being affixed dy a mucous cushion secreted from the extreme tip of the basal cell (Fig. 2), while those of many species of *Ulothrix* are attached by a simple or branched unicellular rhizoid.

The cells vary in size between rather wide limits, being 4·4—9·6 (generally 5—7·5) μ wide, and 22—80 (generally 28—56) μ long, the length being 4—13 (usually 5—9) times greater than the width. There is rarely any variation in the normal cylindrical form—with the exception of the basal and apical cells—although a slight swelling in the middle part of cells about to divide, or which have just divided (Fig. 6), is rather general. The forms assumed by the apical cell are varied; those shown in Fig. 1, 3-5, represent the chief variations observed. A perfectly regular acuminate apex was rather uncommon, the most usual form being the slightly asymmetric and swollen apex shown in Fig. 4, although a more strongly curved and swollen, but always sharply acute, termination such as Fig. 3, was not rare. The cell-wall in the apical part of the terminas cell was sometimes slightly thickened but never markedly so.

The basal cell (Fig. 1, 10) is always very gradually attenuated, and fixed to the subtratum by a small cushion of colourless mucilage, which apparently is a product of secretion of the cell, and is generally encrusted with much foreign matter, and sometimes stained reddish-brown with compounds of iron. The cell-wall of the basal cell is usually somewhat thicker in the lower stalk-like part than elsewhere, and the narrow lumen here is filled with some hyaline pectic substance derived from the cell-wall, and probably the same as that of which the basal mucous cushion is composed. The latter may possibly be secreted through a minute terminal pore, but this point could not be definitely ascertained. The attachment of the filaments to the substratum is not very firm,

Uronema elongatum sp. n.   FIGS. 1-11 × 800.

FIG. 1, apical part of filament, showing the acuminate apical cell ,

FIG. 2, basal part of same filament showing the attenuated basal cell affixed to the subtratum by a mucous cushion ;

FIGS. 3-5, forms assumed by the apical cell of the filament ;

FIG. 6, vegetative division ; in the lower cell the chloroplast has divided prior to cell divisions ; the two upper cells are daughter cells from a recent division ;

FIG. 7, liberation of macrozoogoidia ;

FIG. 7a, free zoogonidium ;

FIGS. 8-10, successive stages in the germination of the zoogonidium to form a new filament, and showing the early formation of the acuminate apex ;

FIG. 11, empty zoogonidangium, the wall of which has become much thickened.

and filaments which had obviously become loosened in some way were not uncommonly seen in samples from the pond, although normally they always remain attached.

No mucous sheath is present round the filaments, the cell-wall being firm, rather thin, the longitudinal and transverse walls generally being uniform in thickness, and with a sharp relief; with iodine and sulphuric acid, or with chlor-zinc-iodine its substance is easily coloured a fine blue, and is therefore cellulose. Each cell has a single parietal bright green chloroplast which is rather small and characterised by occupying only the median part of the cell (see Figs. 1, 2, 10), generally extending $\frac{1}{5}$-$\frac{1}{2}$ ($\frac{3}{4}$) of the total length of the cell, the two ends of the latter being free of chloroplast, while it passes round $\frac{1}{2}$-$\frac{2}{3}$ of the cell's circumference. Its edges are usually very irregular and frequently more or less incised. In the young cell the chloroplast has only one pyrenoid (Fig. 6), but in the older cells the chloroplast almost always has two (rarely three) pyrenoids, each showing a conspicuous starch-sheath, while, in addition, numerous small grains of "stroma-starch" are generally scattered throughout the chloroplast. A small nucleus is suspended in the cytoplasm in the middle of the cell within the fold of the chloroplast; in favourable cases it can be seen without the aid of stains, but in material fixed in weak Flemming's solution its presence can easily be demonstrated by staining with Heidenhain's Hæmatoxylin.

Cell division takes place as in *Ulothrix;* the nucleus divides, and the chloroplast becomes constricted and divides into two equal parts, each with one pyrenoid (Fig. 6), a new cross-wall being formed between the two. Dividing cells are not uncommonly slightly swollen as shown in Fig. 6. The filaments do not readily break up, and vegetative propagation by fragmentation of the filaments does not seem to take place normally.

The only method of reproduction observed was by 4-ciliate macrozoogonidia, which are formed singly in the cells. Any cell —including the apical and basal cells—may function as a zoogonidangium, and in every sample taken from the pond numerous empty cells, showing the lateral pore through which the zoogonidium had escaped (Fig. 7), were seen in many of the filaments, showing that this method of reproduction is the chief, if not the sole, one employed by the alga, during the Spring at any rate. On keeping filaments under close observation in the laboratory for several days the production of zoogonidia was abserved; apparently it takes place exactly as in *Uronema confervicolum.*

In a cell about to produce a zoogonidium the chloroplast becomes rather indefinite, and always shows abundant scattered starch-grains, and (generally) two pyrenoids; the cell contents contracts usually towards the middle of the cell, and rounds itself off, and a somewhat elongated red eye-spot appears. The mass becomes closely applied to one side of the cell-wall, the latter at this spot often showing a slight outward bulge, preliminary to the softening and subsequent dissolution of the cellulose here to form the pore. The latter is generally somewhat narrower than the zoogonidium, which in consequence becomes slightly constricted in its passage through it. The zoogonidium (Fig. 7a) is similar in form to that of *U. confervicolum*, and is broadly ovate, about 13 μ long by 10 μ wide, showing an elongated stigma in the anterior part, 4 cilia, one or two pyrenoids, and an irregular basin-shaped chloroplast. It remains quiescent for some seconds after its emergence, but is not enclosed in a vesicle; the cilia, however, soon become very active, and the zoogonidium swims away.

In many cases it was observed that zoogonidia-formation in a filamint progressed more or less regularly from the apex of the latter downwards, as is often the case in *Ulothrix*,[1] but, as in the latter genus, numerous exceptions to this rule occur. The cell-wall of the empty zoogonidangium sometimes—but not commonly—exhibited curious thickenings, as shown in Fig. 11, the appearance recalling somewhat the structure of the cell-wall in *Tribonema*, although the filaments never become disarticulated as in this genus. Such thickenings of the cell-wall were very rarely observed in ordinary vegetative cells, and they are certainly not a normal feature. Aplanospores, such as are known to occur in *U. confervicolum*, have not been observed.

On germination the zoogonidium loses its cilia, becomes fixed to the subtratum by its anterior end, and, after taking on a thin cell-wall, very soon elongates to the form shown in Fig. 8, the acuminate apex and attenuated base being established very early in the ontogeny of the filament. Fig. 9 shows a very young filament of two cells, while an older filament with a pronounced curvature of the apical cell—a not uncommon feature—is shown in Fig. 10.

An attempt was made to grow the alga in dilute nutrient solution, and also in filtered water from the pond, but owing to the numerous associated filamentatous algæ which outgrew the *Uronema* the latter did not survive long in the cultures, although it formed numerous zoogonidia under these conditions.

[1] Cf. Chodat, Algues vertes de la Suisse, 1902, p. 264.

The alga has since (in June) been found epiphytic on *Cladophora glomerata* growing round the sides of the pool in Victoria Park, Dudley Port, Staffs. In this locality, although it was rather rare, the alga showed precisely the same morphological features observed in the King's Norton material, the filaments, however, apparently not attaining quite the same length as in the latter locality, being generally less than 3 mm. long. The attenuated basal cell was affixed to the *Cladophora* by a mucous pad which was always reddish-brown with iron compounds. The apical cell showed the same variety of forms already described, and was frequently more or less curved. In material which had stood in the laboratory for 24 hours the liberation of the macrozoogonidia was very finely observed, the procedure being exactly the same as in the specimens from the King's Norton pond. It seems probable that the stimulus which caused the formation of zoogonidia was the slight rise in temperature caused by bringing the alga into the laboratory, as is the case, for instance, in *Oedogonium*. The only other algæ observed on the *Cladophora* were many common Diatoms (*Cocconeis Pediculus, Diatoma elongatum, Rhoicosphenia curvata,* etc.), which appeared to be actively competing with the *Uronema* for the available foothold on the *Cladophora*, and a few filaments of *Oedogonium*.

The present species differs from *Uronema confervicolum* Lagerh.[1] mainly in its longer filaments, the much longer cells, and in the chloroplast not occupying the whole length of the cell; in *U. confervicolum* the filaments do not exceed 1 mm. in length, the cells are 10-18 μ long, 4-6 μ wide, and the chloroplast extends the whole length of the cell. The var, *javanica* Möbius[2] of Lagerheim's species differ little from the type. *Uronema ? simplicissimum* (Reinsch) Lagerh.[3] (=*Stigeoclonium simplicissimum* Reinsch[4]) appears to be a doubtful species of *Uronema;* its filaments are 0·84—1·2 mm. long, and the cells 8·4—9·7μ wide, those of the sterile filaments being twice as long as broad, while the filaments terminate in a hair.

Since the present species has both its filaments and cells longer than those of either of the above two species it has been

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[1] Lagerheim in Malpighia, 1, fasc. XII, 1887, p. 518; and in Notarisia, 1888, p. 597; or see Chodat, l.c. pp. 266 and 272, and Fig. 187.

[2] Möbius, Ber. Deutsch. Bot. Ges. XI, 1893, p. 118.

[3] Lagerheim in Malpighia, I, fasc. XII, 1887, p. 522.

[4] Reinsch, Contrib. Alg. Fungol, I, p. 78; or see De Toni, Syll., Alg., Vol. 1, p. 176.

termed *U. elongatum*. Although its cells in general appearance recall somewhat those of a *Stigeoclonium* rather than a *Ulothrix*— with which *Uronema* is most closely allied—yet the alga differs from *Stigeoclonium* in the complete absence of any sign of branching, in the method of attachment to the substratum, and in the characteristic apical cell. The plants of *Stigeoclonium* show either a differentiation of the shallus into a recumbent basal portion, and an erect more or less branched part, or they are attached to the substratum by means of a specially modified basal cell aided by rhizoids, as described by Fritsch;[1] but in either case the method of attachment is different to what obtains in the present alga, which recalls rather the basal rhizoidal cell of *Ulothrix* spp, (*e.g.*, *U. zonata*). No species of *Stigeoclonium* was observed in either of the two ponds.

It has been pointed out by several authors that the genus *Uronema* serves to connect the two families Ulotrichaceæ and Chætophoraceæ.[2] It may be interpreted on the one hand as a stage leading upwards from *Ulothrix* to *Stigeoclonium* and its allies, or on the other hand as a degenerate and permanently unbranched genus derived from the Chætophoraceæ ; or again— perhaps the most probable view—as derived from and standing in close relation to *Ulothrix*, but representing a short and blindly-ending line of evolution.[3] Extensive cultural work on some species of *Uronema* might help to decide this question.

Gaidukov[4] found that a form of *Ulothrix flaccida* Kütz. (=*Hormidium flaccidum* A.Br.), under certain very abnormal conditions in an impure agar culture, developed more or less apiculate end-cells to some of the filaments, recalling somewhat the apical cell of *Uronema confervicolum*. On the basis of his observations he considers that the genus *Uronema* should be included in *Ulothrix* (sens. ampl.). In this he is supported apparently by Oltmanns,[5] and also Wille.[6] However, since the conclusions of Gaidukov were based on impure cultures growing under highly abnormal conditions, and since *U. confervicolum* appears to retain its characteristic features—features never yet observed in any

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[1] Fritsch, Beih. Bot. Centralb,, 1903, p. 368.

[2] *E.g.*, see Chodat, l.c., p. 267.

[3] Compare, *e.g.*, the evolutionary scheme in West's Algæ, Vol. I, 1916, p. 282.

[4] Uber die Kulturen u.d. *Uronema-zustand* d. *Ulothrix flaccida*, Ber. Deutsch Bot. Ges., 1903, p. 522.

[5] Oltmanns, Morph. d. Algen, I, 1904, p. 203.

[6] Wille, Nat. Pflanzenfam. Nachtr. z. Teil I, Abt. 2, 1909, p. 71.

species of *Ulothrix* growing in nature—under widely different geographical conditions, it seems best to keep *Uronema* as a separate genus.

Moreover, Brand[1] has brought forward weighty evidence tending to prove that the pointed appearance of the end-cells of *Hormidium flaccidum* A.Br. observed by Gaidukov is simply due to remnants of shrivelled up intercalary cells which sometimes persist on the terminal cells of broken-up lengths of the filaments.

It is quite possible, however, that a wider knowledge of *Uronema* may show it to be a little more than a sub-genus of *Ulothrix;* and in this connection it is interesting to note that *U. elongatum*, in the length of its filaments, recalls the habit of a *Ulothrix* much more than do either of the other two species of the genus.

The following is a diagnosis of the new *Uronema* :

URONEMA ELONGATUM sp. n. U. filis haud ramosis, rectis, rarius leviter incurvis, usque ad 5 mm. longis ; cellulis basali apicalique exclusis exacte cylindraceis, rarius leviter turgidis, diametro 4-13 (plerumque 5-9) -plo longioribus ; cellula apicali sursum acuminata, at in pilum hand attenuata, plerumque leviter turgida et plus minusve curvata, at interdum tota rectissima ; cellula basali attenuata, pulvino parvo mucoso affixa ; chromatophoro parietali, mediano, $\frac{1}{5}$-$\frac{1}{2}$ (-$\frac{3}{4}$) longitudinis cellulæ complente, pyrenoidibus 1-3 (plerumque 2) prædito.

Propagatio macrozoogonidiis, singulis in quaque cellula oriundis, ciliis 4 instructis, per ostium poriforme cellulæ matricalis evadentibus.

Long. cell. (cell. bas. exc.) 22—80 (plerumque 28—56)μ ;

lat. cel. 4·4—9·6 (plerumque 5—7·5)μ ;

long. cell. basal. 60—90μ.

Hab. in stagno parvulo, King's Norton, Birmingham, in *Oedogonii* sp. et plantis phanerogamis aquaticis (*Myriophyllo, Lemnæ minoris* radicibus) epiphyticum ; etiam in stagno, Victoria Park, Dudley Port, Staffs, in *Cladophora glomerata.*

In conclusion I wish to express my thanks to Prof. G. S. West for very kindly examining the alga for me, and also to Mr. W. B. Grove, M.A., for his kind help in connection with the literature.

[1] Brand, Ber. Deutsch. Bot. Ges., Vol. XXXI, 1913, p. 69.

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ON THE NATURE OF FERTILIZATION AND SEX.

By W. NEILSON JONES, M.A.

(*Lecturer in Botany, Bedford College.*)

THE essential fact in the process of fertilization is that a male gamete fuses with a female gamete to produce the zygote. This fusion is probably the result of a definite chemical attraction, and in some cases the chemical nature of the attracting substance would appear to have been identified.

Thus, in the ferns, malic acid has been credited with this *rôle*, and the attraction of the motile spermatozoids to the archegonia and egg-cells has been imitated by filling a small capillary tube, closed at one end, with malic acid and dipping the open end of the tube into a drop of water containing the spermatozoids.

Another characteristic of the phenomenon of fertilization is that the egg-cell, containing an abundant store of nutriment, is inert until fusion with the male gamete occurs, whereupon rapid cell division at once ensues.

Sexual reproduction in general is evidently closely correlated with nutrition, and appears to be in some measure a starvation phenomenon. This may be recognised in its simplest form among unicellular organisms. In the case of the free-swimming unicellular alga *Chlamydomonas*, individuals which normally, in the vegetative state, lead independent lives, under starvation conditions develop a mutual hunger and fuse in pairs, or, according to the species, exhibit various degrees of sex differentiation, expressed by the relative activity and passivity of the fusing cells.

These phenomena of fertilization appear to the writer to be not peculiar to fertilization, but to be of the same kind as those which characterise parasitism, symbiosis and the reactions of living protoplasm in general.

Let us consider fertilization from this point of view and see
how far the opinion may be justified. Thus regarded, fertilization,
in all but the most primitive organisms, resolves itself into the
" attack " of a " parasitic " male gamete upon a female gamete well
stocked with food reserves. As in cases of parasitism the " host "
exercises a chemical attraction upon the " parasite " (viz.: the
male gamete), as a result of which the " parasite " cell penetrates
the " host " cell and their respective protoplasms come into direct
contact with one another.

In parasitism of the ordinary kind, the destruction of the
tissues of the host may be rapid and complete—the tissues being
killed and demolished forthwith. More generally the host cells
react as to a stimulus, such reaction being expressed by greater
cell activity, leading in many cases to the formation of warts and
swellings and other distortions of growth. Stimulation of this
kind is a common and widespread accompaniment of parasitic
invasion of tissues, and the hypertrophy or local overgrowth
which frequently results from it is a well known phenomenon.
Among vascular plants the numerous cases of gall-formation,
distortion of growth, or excessive branching leading to the forma-
tion of the so-called " witches brooms " in trees, may be cited as
familiar examples of such response to invasion of the tissues by
foreign organisms. Anatomically, swellings of this kind may be
formed entirely from the tissues of the host, as for instance is the
case in plant galls produced as the result of oviposition by various
insects, or they may be of a composite nature, consisting of the
tissue of the host intermingled with that of the invader, as in the
nodules formed by many plants as a consequence of invasion of
the tissues by bacteria or fungi.

It does not seem unreasonable to regard the growth stimulus
resulting from fertilization as, essentially, of the same nature. The
result of the stimulus of fertilization in multicellular organisms is
the formation of a complex of dividing cells. In unicellular
organisms, such as *Chlamydomonas*, a corresponding activity is
shown, but the individual cells separate as they are formed instead
of building up a mass of tissue.

Another well marked characteristic of fertilization is that
normally the egg-cell is fertilised by one male cell only. The
behaviour of the sex cells in the brown seaweed *Fucus*, studied in
detail by Farmer and Digby, will serve as an example.

If an unfertilized egg-cell of *Fucus* is examined under the

microscope in a drop of sea water in which male gametes are swimming, the latter are seen to cluster closely round the egg-cell (no doubt attracted chemically) often in such numbers as to cause it to undergo considerable movement. Eventually one spermatozoid enters the egg-cell, whereupon the egg-cell ceases to attract the remainder of the spermatozoids. One explanation offered for this change of mutual reaction is that after fertilization the egg-cell excretes a cell wall, thus cutting off communication with the outside world, It would seem unlikely, however, that a cell wall of such a nature as would prevent the egress of the attractive substance from the egg-cell could be formed so instantaneously, and it is more probable that the change in reaction is the result of chemical causes, *e.g.*, gametic fusion brings to an end the production of attractive substances, or even leads to the production of substances whose action is repellant to the remainder of the male gametes.

This explanation receives support from results obtained in experiments with sea-urchins' eggs conducted with the object of bringing about double fertilization. From such experiments it appears that it is possible to induce more than one spermatozoid to enter the egg-cell if the vitality of the latter be suitably lowered either by chemical or physical means.[1] One may compare the results obtained by Salmon in his experiments on the susceptibility of grasses to fungal attack under varying conditions. It was found that a variety of grass which was immune to attack by a particular fungus might become susceptible if the vitality (and therefore resistance) of the individual were lowered artificially. So far as double fertilization of the egg-cell is concerned, the facts may be stated in the following way: the fertilized egg-cell is immune to attack from spermatozoids under normal conditions; if, however, its vitality is lowered, resistance is decreased and it may be rendered susceptible to attack by a second spermatozoid.

The "double" fertilization" occurring in the embryo-sac of angiosperms may be described in somewhat similar terms. The

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[1] Compare results obtained in experiments on hybridization of Echinoids. Thus Doncaster (Experiments in Hybridization, Phil. Trans. B. Vol, CXCVI., 1903), states that " cross fertilisation is assisted by conditions which tend to reduce the vitality of the eggs." Similarly Loeb (" Ueber die Befruchtung von Seeigeleiern durch Siesternsamen," Pflüger's Archiv. Vol. XCIX., 1903, also Vol. CIV., 1914), found that cross fertilisation between *Strongylocentrotus* and *Asterias*, which occurred very rarely in normal sea water, could occur to the extent of 50 per cent. if the sea water were made slightly alkaline by addition of Na_2CO_3 or $NaOH$.

male nucleus and one polar nucleus, instead of forming an exactly balanced system, still possess an attraction for (or are attracted by) the second polar nucleus. The case is, in fact, almost the converse of that in which the egg-cell is fertilized by two spermatozoids. As a result of the triple fusion there is produced not a stable organism but a growth comparable to those resulting from parasitism—a growth which forms the endosperm.

One may draw attention here to certain important and surprising results that have been obtained in the course of experiments with sea-urchins' eggs. It has been found that unfertilized eggs can be "fertilized," or at least their development initiated, by purely chemical means—by immersing the eggs in solutions of certain salts. In some cases development has been brought about even by the mechanical operation of pricking the egg-cell with a needle. The egg-cell is not, therefore, dependent for development on the spermatozoid *qua* spermatozoid, but merely on the stimulus that is imparted to it by the entry of the latter.

The stimulus to cell division imparted to the egg-cell by entry of the spermatozoid is thus in its results not unlike that imparted to the embryo of certain plants, such as the orchids, by infection of the seedling with the mycorhizal fungus. In neither case does cell division occur until the stimulus resulting from the presence of the missing member of the dual alliance is provided : as soon as this is applied normal growth proceeds. In the case of the egg-cell the normal stimulus can be imitated, in rare cases, by other and artificial means: an appropriate artificial stimulant has not been discovered yet for those curious cases in which there is arrested development of the seedling pending infection by the mycorhizal fungus. This difference of behaviour is probably more apparent than real, for it would seem relatively more simple to cause an orchid embryo to commence growth by substituting direct chemical stimulus for fungal infection, than to initiate development of an unfertilized egg-cell by the substitution of an artificial stimulus for that which results normally from fertilization by a male gamete.[1]

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[1] Some work of Calkins upon *Paramœcium* is of interest in this connection as illustrating the use of an artificial stimulant in place of the one naturally occurring in a case of arrested development (" Studies in the Life History of Protozoa IV." Jour. of Exper. Zool. Vol. I., 1904). Maupas had shown that in *Paramœcium* the vigour and rate of vegetative reproduction gradually decreased in cultures, but was regained as the result of conjugation between two individuals. If this conjugation were prevented the individuals ceased to divide altogether and eventually died. Calkins found that the loss of vigour, which invariably occurred if conjugation were prevented, and led normally to a cessation of cell division and death, could be tided over and the race carried through further cycles of activity, by the use of artificial stimuli. By using extracts of beef, pancreas, etc., the race was carried on through four cycles of activity, *i.e.*, past three depression stages.

It must not be forgotten that cases are known in which egg-cells develop regularly without fertilization, just as the majority of plant embryos develop without the stimulus of fungal infection ; but ova which behave in this way are exceptional and in most cases not the cytological equivalents of normal ova. The rule and exception in the two cases are inverted.

Let us consider for a moment the position which has now been reached.

The point of view advanced is that the male and female gametes in fertilization stand to one another in a relation corresponding to that occupied by parasite and host, or perhaps more accurately to that existing between the two components in cases of balanced parasitism or " symbiosis," many examples of which can be cited from the plant and animal kingdoms.[1] Using the language of pathology, it may be said that the egg-cell is susceptible to attack by the male gametes of the same species, but that the zygote is immune following entry of a male cell into the ovum. One is almost tempted to say that the egg-cell after fertilization has been " vaccinated " against a further attack from spermatozoids !

The stimulus to cell division which the egg-cell receives from union with the spermatozoid has been likened to the stimulus to development the embryos of certain plants receive from infection by the mycorhizal fungus—in neither case can growth occur without the application of the respective stimuli, except in special and rare cases.

It is possible to extend this comparison of fertilization phenomena with the general mutual reactions of protoplasm. There are many cases of plants with dimorphic flowers in which legitimate unions are fertile and illegitimate unions more of less sterile. The relationship in the case of *Primula* may be expressed in the following way according to the present hypothesis.

The egg-cells produced by plants with " pin eyed " flowers are susceptible to attack by the male gametes from plants with " thrum-eyed " flowers, but immune from attack by those from " pin-eyed " flowers. Conversely, the egg-cells produced by " thrum-

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[1] Every stage may be found of a series having at one end a purely destructive parasite, against the attack of which the host plant seems able to offer little resistance, and the " parasite " that lives side by side with its " host," the relations between the two being so nicely balanced that the attacking power of the one is just compensated for by the limited immunity of the other. A further development of the immunity of the " host " leads to the partial or entire exclusion of the potential parasite.

eyed" flowers are susceptible to the male gametes from "pin-yed" flowers and immune to male gametes from "thrum-eyed" flowers. From the point of view now under consideration such behaviour may be interpreted as a special case of differential immunity, other instances of which are known (*e.g.*, in the orchids, the root system is susceptible to infection by the mycorhizal fungus, while the immunity of the shoot system excludes the fungus from this part of the plant).

The difficulty in obtaining seed as the result of pollinating one plant species with the pollen from another species is capable of a somewhat similar explanation, viz.: the egg-cells are susceptible to attack by male gametes of the same species but, in general, immune to gametes from another species. It must not be forgotten, however, that failure to set seed when species are crossed may be due to lack of attraction as well as to the presence of a definite immunity on the part of the egg-cell, just as may the freedom of a plant against infection by a specific parasite. The variability as to sterility found in different varieties of a species finds an obvious parallel in the varying susceptibility and immunity of varieties to attack by parasites, as is to be seen for example in the " biologic races " of grasses described by Salmon (*loc. cit.*).

The "plus" and "minus" races of *Phycomyces* and other members of the Mucorineæ investigated by Blakeslee can be evidently described in the same terms and may be analogous in nature.

On the present hypothesis the origin and evolution of sexuality becomes closely bound up with those of parasitism. The earlier forms of life were inevitably holotrophic, and from these were evolved organisms whose protoplasm reacted mutually in the manner characteristic of parasite and host. An advanced stage of such evolution is represented by plants, such as the orchids, in which the stimulus of infection by a fungus is necessary before development of the seedling can take place, or by those obligate parasites which require a specific host.

The most primitive form of reproduction in unicellular plants is by simple fission, and this becomes elaborated into the pro-duction of asexual spores. Among the green and brown Algæ can be traced an almost continuous series leading from such spores to gametes morphologically, and in many ways physiologically, alike; and ultimately to cases where the gametes show differentiation into a larger non-motile female cell and a smaller actively free-

swimming male cell. In the Algæ, therefore, both male and female gametes may be regarded phylogenetically as special kinds of spores: a complete series occurs in which the protoplasm in the species becomes more and more highly differentiated into two sorts—greater differentiation being accompanied by more and more dependence upon fusion before the reproductive bodies can carry on development. The case is, in fact, comparable to that of a series of hemiparasites which show more and more dependence upon a suitable host, or to a symbiotic partnership in which the partners show greater and greater dependence upon one another, together with an increasing degree of mutual adaptation.

It may be pointed out that although the egg-cell is usually spoken of as requiring the stimulus of fertilization by the male cell before it can develop, it would be just as true to say that the spermatozoid requires an egg-cell which it can enter (" parasitize ") before it (the spermatozoid) can develop. Regarded from this latter point of view, the phenomenon occurring in fertilization is analogous to that observed when an obligate parasite requires an appropriate host before it can carry on its growth.

What causes have been responsible for the differentiation of protoplasm into two kinds (male and female) in the course of evolution—such as appears to have occured for example in the genus *Chlamydomonas*—it is not yet possible to say ; but one may evidently regard the sex differentiation of the individuals which behave as gametes in a single species such as *C. Braunii,* or the differentiation of the gametes in any of the higher plants during the lifetime of the individual[1] (for both of which examples the same kind of forces are evidently responsible) as special cases in which the evolutionary history of the race plays a part in the ontogeny of the individual.

The evolution of sexuality with its accompanying phenomenon of fertilization may be regarded, therefore, as the evolution of mutual parasitism within the species: and, indeed, since the difference involved in the differentiation of the two kinds of protoplasm distinguishing the sexes of a species would appear to be less than that involved in the differentiation of one species from another, one is tempted to alter the form of the above statement and to suggest that the evolution of sexuality may have been the first step towards the evolution of parasitism.

[1] In comparing a unicellular organism with one that is multicellular, it must be remembered that the cells which result from vegetative division remain united to form the " individual " in the latter case, while in the former each cell becomes a free "individual."

It is believed that a good case has been made out for regarding many of the phenomena that accompany fertilization as manifestations of the same general protoplasmic reactions which are exhibited in the behaviour of parasite and host towards one another in cases of parasitism or in the mutual reactions of the two components of a symbiotic alliance.

If this view be accepted, it becomes of interest to speculate as to what lengths it is possible to push the comparison. For instance, a lichen consists of the balanced association of a " host-like " and a "parasite-like " partner. In what degree can one regard the zygote as an organism built up of two partners— the male and female gametes—whose association is more intimate and the balance between which is even more delicately poised ? Before dismissing such an idea as fantastic let us examine the points of resemblance more closely.

A lichen is built up of two partners, and although the association is an intimate one, the two components can always be recognised histologically, since each retains its own cell wall. In cases where symbiosis occurs between an animal and a plant, as in the association between an animal such as *Convoluta roscoffensis* and a unicellular green plant, the delimitation of the two components one from the other is often readily to be observed owing to the well defined cell wall possessed by the plant cells. In this case, had the cells of the plant partner been naked and amœboid, it is conceivable that the association would have been much more intimate and more difficult to resolve into two separate organisms.

In point of fact there is frequently considerable difficulty in recognising histologically that two organisms are involved in cases of parasitism or symbiosis, so close may be the adaptation between the individual cells, or so great the reduction of one or other of the components in certain regions. This is the case, for instance, with the " smut " fungus when growing in the vegetative tissues of its host, or with the mycorhizal fungus in the stem and leaf tissues of *Calluna vulgaris*. In other cases, again, it has been suggested that two organisms are involved although no proof can at present be adduced of their existence. The somewhat fantastic suggestion that the chloroplasts of the higher green plants are phylogenetically derived from invading algal cells, or—in the region of animal pathology—the view that an individual suffering from small-pox, or measles, or scarlet fever is a victim of parasitic, invasion would be cases in point.

Now the zygote is built up of the union of two cells of physiologically different nature. The reactions that occur between the protoplasts of these two cells have been shown to resemble in many ways those manifested between parasite and host or between the two members of a symbiotic alliance. Can the zygote be included among such cases as those just cited? Is there any evidence that the zygote (using the term to include the product resulting from the development of the fertilized egg-cell) is in reality a dual structure, and is it possible to recognise the two "partners" forming it, after union has occurred at fertilization?

From cytological evidence it appears that the maternal and paternal components of the nucleus may retain their identity, as manifested by the behaviour of the chromosomes, although both are in the same "cell." Among the copepods, for example, the maternal and paternal chromosomes may retain their own spindles for many successive nuclear divisions and the dual nature of the cell structure be very evident.

One may say then that the dual nature of the fusion-product is not, of necessity, immediately and entirely obscured, though more evident in some cases than in others. The cytological evidence is not incompatible with the view that the zygote, at least during the early stages of development, is to be regarded as a dual organism, the constitution of which is analogous to that of a symbiotic partnership in which the cells of the two partners are not delimited from one another by cell walls as are the cells of plants, and the association between whose protoplasts is extremely intimate.

If the zygote may be so regarded during the early stages of its development, there are no logical grounds for refusing to extend this conception to the whole of the life-history, though the degree of intimacy between the two components may vary at different times. It is significant that the behaviour of the chromosomes during meiosis suggests that the nucleus is a double structure; and that cytologists in general agree that the "individuality" of the chromosomes—and therefore presumably the double nature of the nucleus—is maintained during the so-called resting phase of the nucleus. The assumption that the cells of the zygote remain double in structure is also involved in an acceptance of the Mendelian scheme of inheritance.

To regard the cells of the zygote as dual in nature is thus not unorthodox.

The process of fertilization, then, may be compared with the building up of a symbiotic dual organism in which the two partners are differentiated by the reactions of the protoplasm of which they are composed. It is assumed that the two kinds of protoplasm are found isolated, or nearly so, in the male and female gametes[1] from which the dual organism arises. For the sake of convenience of reference the respective characteristics of the two kinds of protoplasm will be compressed, in the following discussion, into the terms "active" and "passive" (*cf.* the relations between parasite and host).

It is not intended to suggest that "activity" and "passivity" are the only differentiating traits exhibited by the two kinds of protoplasm, and when the terms are employed they must be understood to imply two groups of characteristics, of which "activity" and "passivity," although usually well marked or easily recognisable, are only one pair.

When fusion occurs at fertilization, an intimate mixture of "active" and "passive" protoplasm results and, in plants, definite bodies such as plastids[2] previously contained within male or female gametes now find themselves within a single "cell" composed of the "mixed" protoplasm. At certain cell divisions occurring during the development of the zygote, it is conceivable that the coarser elements in the cell may become segregated while the finer ground-substance remains essentially uniform. Baur explains the occurrence of the green and white mosaic areas of certain variegated plants (*e.g., Pelargonium*) along such lines.

Similarly, there seems no reason why the segregation of the chromosomes, if these can indeed be regarded as definite entities (or as composed of definite entities) distributed in the mixed protoplasm, should not occur without necessitating a separation of the zygote into its "active" and "passive" protoplasmic components.

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[1] In the higher animals and plants, it has been questioned whether any cytoplasm accompanies the male nucleus into the egg-cell at fertilisation. V. H. Blackman, however, has shown that this occurs in the case of *Pinus*, while the genetical behaviour of certain variegated races of *Pelargonium* has received explanation on the same supposition (Baur). Even if no cytoplasm accompanies the male nucleus, the nucleus itself consists of a comparatively homogeneous ground-work in which the chromosomes are distributed. It may well be that this general nuclear ground-work is responsible for the manifestation of "active" or "passive" characteristics exhibited by the gametes. Experiments shewing that enucleated fragments of egg-cells attract spermatozoids shed little light on this question.

[2] Among the more primitive groups of plants, such as the Algæ, the male gamete is usually provided with one or more plastids: in the higher plants, however, the male gamete is not obviously accompanied by plastids. (See previous note).

At fertilization the protoplasts of the male and female partners unite to form the zygote and at the same time the number of chromosomes, etc., becomes doubled.[1] At some subsequent stage of development the number of chromosomes becomes halved owing to the occurrence of a " reduction division," but there seems no reason why this should necessarily involve a separation of the " active " and " passive " elements of which the organism is built up.

To state the matter more explicitly, it is not suggested that the " active " and " passive " types of protoplasm, which, as partners, build up the zygote, are homologous with the Mendelian factor-carriers or with the two sets of chromosomes, but rather that they form a mosaic groundwork within which the latter more definite bodies occur.[2]

An analogy, even though somewhat crude, may help to make the conception clearer.

Suppose the "active" and "passive" types of protoplasm to be represented by alcohol and water and the two sets of chromosomes by iron and brass filings suspended in these liquids. If we mix the two suspensions there results an intimate mixture of alcohol and water and a mixture of iron and brass filings. By the use of a magnet it would be easy to separate the fluid into two portions, one containing iron filings and one brass filings. This would correspond to the segregation of chromosomes that occurs at the reduction division. The operation would not necessarily involve the separation of the alcohol from the water. For this, other forces, such as those employed in the process of distillation would be required.

Thus, although the same act of mixture was responsible for bringing about the double nature both of the fluid and of the filings, the process causing the separation of the filings does not

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[1] Doubled, if there are the same number of chromosomes in male and female gametes.

[2] The duality of the organism, as regards the number of chromosomes, ceases at the " reduction division " characteristic of meiosis, which occurs at some definite stage in the life history. The duality in respect to hereditary characters is brought to an end, normally, at the same time (wherefore the supposition that such characters are carried by the chromosomes). But nevertheless the character factors would appear to be independent to some extent of meiosis in view of the occurence of phenomena such as somatic segregation and reduplication. Lastly, as suggested below, the separation of the protoplasmic partners is independent of either of the above segregations, and although occurring some time before the formation of gametes, may take place at different stages in the life cycle, according to the nature of the organism.

cause a separation of the fluids. On the lines of this analogy, the process of fertilization leads to the formation of the "symbiotic organism"—the zygote—from "active" and "passive" varieties of protoplasm, and, at the same time, brings about the doubling of the number of chromosomes: the reduction division leads to the separation from one another of the two groups of chromosomes that came together at fertilization, but need not separate the "active" from the "passive" type of protoplasm, or in other words, dissolve the hypothetical symbiotic partnership.

It would seem necessary to assume however that the two kinds of protoplasm do become differentiated previous to, or simultaneously with, the formation of sex cells or gametes, since in these cells can be recognised once again the marked "activity" and "passivity" characteristics.

The life history of a plant such as an homosporous fern on this basis will be as follows:

The male and female gametes, consisting of "active" and "passive" varieties of protoplasm (with nuclei, etc.) unite to form a symbiotic partnership in the zygote. This partnership persists throughout the life of the "sporophyte" and throughout the formation of spores (which is accompanied by reduction in the number of chromosomes). The spores germinate to produce the prothallus (gametophyte) still with the duplicate type of protoplasm. At a certain stage the prothallus produces antherozoids and egg-cells; and since these exhibit the characteristic "active" and "passive" traits and a readiness to combine again, we must suppose that their production has involved once more segregation into the two kinds of protoplasm.[1]

If a flowering plant be considered from this point of view—choosing a dioecious species as simplest for purposes of discussion —one is met at once by difficulties arising from the confusing terminology ordinarily employed.

[1] E. J. Collins has recently described some interesting experiments that are suggestive as to the stage in the life cycle at which sexual segregation may occur in the Bryophytes (Linnean Society, June 20th, 1918). Cultures of *Funaria hygrometrica* were made and (a) protonemeta were grown from antheridia and from perigonial leaves of male "flowers"; (b) plants were raised from spores from a ripened capsule. Submitted to similar cultural conditions (a) produced a sward of plants with male "flowers" *only*, no sporogonia being formed at any time, whilst (b) produced plants bearing both male and female organs. Thus in this case, segregation of male protoplasm would seem to occur before the actual production of antheridia or antherozoids. As is pointed out by the author, the shifting backwards in the life cycle of the point at which segregation occurs until it is coincident with sporogenesis would result in a Bryophyte with the "dioecious" habit.

The plants ("sporophytes") are said to be of two kinds—"male plants" and "female plants." As the reference is to the sporophytes, terms signifying sex should not, strictly speaking, be employed, but the two kinds of plants should be described as "microspore-producing" and "megaspore-producing." Since the microspores normally produce male gametes (with "active" type of protoplasm) and the megaspores normally produce female gametes (with "passive" type of protoplasm) the sex terms, which should be reserved for the gametes, have come to be applied to the sporophyte by a process of mental short-circuiting and for the sake of brevity.

It is very necessary, in a discussion such as the present, to distinguish with the greatest clearness between the so-called "sex" of the sporophyte and the sex of the gametes. One way of accomplishing this would be to place the words "male" and "female" within inverted commas when they were intended to signify a microspore-bearing or megaspore-bearing individual, while male and female without inverted commas would be understood to refer to the male and female gametes, or other tissues composed of "active" and "passive" kinds of protoplasm. Indeed, the complete disuse of the words "male," "female" and "sex" in respect to the sporophyte of a plant is logically called for, as the gametes undoubtedly have a preferential claim to the use of these terms. Nevertheless, their usage in the former relation has become so general that the prejudice against restriction of use to the gametes alone, however reasonable on purely logical grounds, would be wellnigh insurmountable. Yet some distinctive terms must be employed unless we are to be involved in hopeless confusion.

The following conventional system of nomenclature will be made use of for purposes of discussion as providing a way out of the *impasse* without prejudice to any more satisfactory solution that may be forthcoming subsequently.

The two kinds of protoplasm ("active" and "passive") are designated "androplasm" and "gynoplasm." The protoplasm of a spermatozoid is therefore "androplasmic," that of an egg-cell "gynoplasmic": while the spermatozoids and ova, instead of being called male and female gametes, are called "androplasmic gametes" and "gynoplasmic gametes" respectively. The terms "male" and "female" are retained for use in connection with the sporophyte of the plant, as signifying a microspore-producing or megaspore-producing individual and are used *only* in this sense,

Also, by the "sex" of a plant is understood the kind of spores it produces—spermatozoid and egg-cell differences being distinguished from the above sex (sporophytic) differences as differences of "gender."

The same distinctions may be drawn with respect to the animal kingdom, the only difference being that the vegetative phase of the gametophyte is entirely suppressed from the life cycle. For this reason it is convenient to confine the discussion which follows as far as possible to plants, as representing the more general case. The same arguments may be applied, however, to animals.

Summarising, the sporophytes differ in "sex," while the gametes differ in "gender": the sporophytes are of the "male" (microspore-producing) sex or of the "female" (megaspore-producing) sex, while the gametes are of the "androplasmic" ("active") or "gynoplasmic" ("passive") gender—male and female being terms employed *only* in reference to the sporophyte. These special and restricted uses of terms will be adhered to throughout the remainder of this article. Under this scheme the higher animals differ in "sex" (being male or female) in accordance with ordinary practice.[1]

Having made this distinction clear, one is now in a position to proceed further.

A large amount of breeding work has shewn that somatic (sporophytic) character factors may be carried indifferently by either androplasamic or gynoplasmic gametes and that a somatic character factor which entered the sporophyte with the andro-plasmic gamete may be carried by a gynoplasmic gamete when the time comes for the individual to produce reproductive cells.

Hence it would appear that somatic character-factors may segregate without reference to the differentiation of the androplasmic

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[1] The Editor has reminded me of Strasburger's theory of "kinoplasm" and "trophoplasm" put forward in 1892 (Histol, Beitr., IV). It will be remembered that kinoplasm is the active "moving" element specially sensitive to external stimuli, while trophoplasm is the food-making element. The resting cell consists of both kinoplasm and trophoplasm, the former being localised chiefly in the "tonoplast": in the dividing cell the kinoplasm becomes evident in the karyokinetic spindle. The cilia of a zoospore and the "mundstelle" to which they are attached consists of kinoplasm, and the body of a spermatozoid, which is a reduced zoospore, consists mainly or entirely of kinoplasm, the reduction affecting the trophoplasm alone. The similarity with the "androplasm" and "gynoplasm" proposed in the present article had not occurred to me previously, but the resemblance is certainly striking, although Strasburger was concerned with general protoplasmic activities and not with reproductive phenomena when he postulated two kinds of protoplasm. It would seem very probable that the "kinoplasm-tropho-plasm" and "androplasm-gynoplasm" conceptions are different aspects of the same thing.

and gynoplasmic components of the organism. Other breeding work suggests, as Castle pointed out, that the sex of the sporophyte behaves in inheritance as though it were a unit character, obeying the ordinary Mendelian rules like any other unit character. Cytologists also have shewn that this sex is associated in certain animals with the occurrence of a special chromosome. If sex is really of the same nature as any other unit character, the factors for it must be carried indifferently by either kind of gamete; and the hypothesis that the sex factors are so carried is supported by the cytological observation that the sex chromosome may be carried either by spermatozoid or egg-cell.

The sex, then, of a dioecious flowering plant would appear to be dependent on the presence of certain sex factors which behave as do other Mendelian factors in reproduction and *are carried indifferently by either gamete.*

These sex factors cannot therefore be the agents that determine the nature of the gametes themselves—whether these are spermatozoids or egg-cells—exhibiting the features of " active " or " passive " protoplasm.

Thus one must postulate the existence of two sets of " factors " :

1. Those determining the sex characters of the sporophyte. These are inherited according to the ordinary Mendelian scheme and are carried indifferently by either gamete, probably by the chromosomes of the nucleus. Such sex factors cannot determine the nature of the gametes—whether these are androplasmic (" active ") or gynoplasmic (" passive.")

2. Those determining the character of the gametes themselves, whether these are androplasmic or gyno- plasmic, *i.e.,* composed of " active " or " passive " protoplasm.

Consider, now, in the light of the above, the life history of a simple organism, such as the unicellular green plant *Chlamydomonas.*

A zygote is formed by the union of two cells functioning as androplasmic and gynoplasmic gametes, *i.e.,* a portion of " active " protoplasm unites with a portion of " passive " protoplasm to form a balanced or " symbiotic " product. This then undergoes successive divisions forming a series of free cells. (In multicellular plants the same process occurs, but the resulting cells do not separate from one another).

After a time however the balance between the two cell components ceases to be so well adjusted and one begins to gain an ascendancy either through its *quantitative* increase or because it has become more virulent in *quality* (cf. the way in which the balance of the ordinary symbiotic organisms can be disturbed by one partner becoming more virulent under certain conditions of culture).

Thus the protoplasm becomes more androplasmic ("active") or gynoplasmic ("passive") in quality and the cells reach a condition in which they are ready to fuse again, that is to say the protoplasm of the two cells becomes sufficiently unlike for them to function as gametes. The rapidity with which the androplasmic and gynoplasmic types of protoplasm become thus differentiated or segregated will depend doubtless in some degree on the environmental conditions, supply of nutriment, etc. In multicellular plants, special conditions of nutriment, etc., occur in different regions, so that one would expect that certain regions of the plant organism would show a special tendency towards the differentiation into the two kinds of protoplasm, *i.e.*, towards the formation of gametes of one kind or the other.[1]

In the higher plants, for example, the conditions occurring in the anthers or microspores appear to favour specially the development of the androplasmic type of protoplasm, while the conditions in the embryosac tilt the balance in the opposite direction and favour the differentiation of gynoplasmic protoplasm. Whatever the actual causes may be, similar forces are probably ultimately responsible both for the differentiation of the gametes from the general body of the multicellular plant and for the differentiation and determination of the gender of the gametes that occurs in a single species of *Chlamydomonas*, such as *C. Braunii*.

In the case of a flowering plant the complete cycle will be as follows. The androplasmic and gynoplasmic gametes, uniting at fertilisation, establish in the zygote the symbiotic partnership of "active" and "passive" varieties of protoplasm. This partnership persists throughout the development of the zygote (sporophyte), including the formation of the flowers with their anthers and ovaries. The segregation into androplasm and gynoplasm does not occur, probably, until (or shortly before) the

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[1] Compare *Vaucheria*, etc., in which, as shown by Klebs, the occurrence or inhibition of reproduction and the nature of the reproductive cells is directly correlated with external conditions.

production of gametes with their characteristic "active" and "passive" protoplasm. That is to say, both megaspores and microspores still contain the two kinds of protoplasm, although it is not improbable that the environmental condition may have already weighted the balance on one side or the other.[1]

The fact that some plants are hermaphrodite and some diœcious, etc., has nothing to do directly with the present problem, since the production of anthers or ovaries is a sex or somatic (Mendelian) characteristic, which may show somatic segregation like other somatic characters.[2]

The only interest the sex distribution possesses in the present connection is that the archesporial tisssue of the anthers is predestined normally to develop into microspores, an environment which favours the dominance of "active" or androplasmic protoplasm : and *vice versa* for the archesporial tissue of the ovules.

It may be noted that, if the gametes consist of *pure* androplasm or *pure* gynoplasm, then a normal egg-cell, if induced to develop without fusion into a mature individual, should be incapable of producing androplasmic gametes. If such an apogamously produced individual were found to give rise to androplasmic gametes, the presumption would be that both varieties of protoplasm were present in the gynoplasmic gametes, but that the "passive" variety predominated—the converse holding for the androplasmic gametes.

Phenomena such as apogamy can be fitted into the scheme suggested without difficulty, since the gametophyte still contains both "active" and "passive" varieties of protoplasm, although segregation of chromosomes and sex factors has taken place. With regard to the hypothetical segregation of the two kinds of protoplasm when gametes are formed, it may be worth calling attention to one of the theories that have been brought forward to account for the occurrence and behaviour of cancerous growths in animals. According to this view the forma-

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[1] See note p. 18 regarding time of segregation in Bryophytes.

[2] The monœcious or hermaphrodite habit may be likened to the condition obtaining in a plant which is heterozygous for some Mendelian factor and in which somatic segregation occurs such that one allelomorph appears pure in one region of the plant and the other allelomorph in some other region. Thus the distribution of " rogue " and " type " characters in certain races of peas, so that the former characters are dominant in the upper part of the stem and the latter at the base, is suggestive of the somatic segregation of sexes occurring in the inflorescence of plants such as *Typha*. The diœcious habit is more comparable to normal Mendelian segregation, where the individual is either pure dominant or pure recessive. The matter is in reality less simple than this, however, since there is much evidence to show that in a female plant maleness is suppressed rather than absent.

tion of a cancer is due to the rejuvenescence of certain cells—these cells becoming free from the correlation that normally controls the growth of the organism and leading an independent existence as a parasite upon the rest of the tissues. Is it possible that this may be a manifestation that the balance between the two protoplasmic components has been disturbed, that cells of the potentially "active" kind have lost correlation with the tissues as a whole and become parasitic on the symbiotic organism in the same way that the mycorhizal fungus of a mycorhizal plant may become parasitic upon the plant when the resistance of the cells of the latter has been impaired or lowered? The fact that a correlation has been established between certain types of cancerous growths and the presence of specific poisons or stimulants is in harmony with such a view.

It is convenient at this point to summarise the propositions that have been put forward in the course of this article. These are :—

1. The phenomena of fertilisation show so many points of resemblance with those of parasitism and symbiosis that the one is probably only a special case of the other.

2. Cytological and genetical evidence, as well as mode of origin, points to the zygote having a dual structure, which has been likened to a symbiotic organism in which the partners are androplasm or "active" protoplasm, and gynoplasm or "passive" protoplasm, derived from the respective gametes.

3. These two varieties of protoplasm are found more or less pure in the gametes, *i.e.*, the mixed protoplasm becomes differentiated into its two component parts at or before the formation of the gametes.

4. Two sets of so called "sex" determinants must be distinguished.

    (*a.*) Sex factors which determine the sex characteristics (*e.g.*, type of spore production in the case of vascular plants) of the hypothetically symbiotic organism.

    (*b.*) Those which are responsible for the differences, such as relative activity and passivity, shewn between the protoplasm of androplasmic and gynoplasmic gametes (gender factors).

The former, (*a*), obey the ordinary Mendelian scheme of inheritance and are carried indifferently by either gamete, upon the nature of which they cannot therefore have any influence.

The latter, (*b*), determine the characteristics of the gametes, but have no necessary correlation with the Mendelian character factors carried by the gametes.

Although the sex factors may not directly influence the nature of the gametes, the converse is not necessarily true.[1] It remains to enquire whether the gender factors which determine the nature of the gametes have any influence upon the character of the zygote.

In a symbiotic organism such as a lichen, one may expect the plant to show variations in the direction of being more algal or more fungal in nature, in accordance with the characters of the strains of alga and fungus entering into its composition, and this is indeed the case. Similarly the zygote, if its dual structure be admitted, might be expected to exhibit variations as regards " activity " or " passivity "—the exact position of equilibrium between the two tendencies which characterise the gametes depending upon the strains of androplasmic and gynoplasmic protoplasm that combined at fertilization. This, be it noted, has nothing whatever to do with the sex of the organism (zygote) which is controlled by the sex factors—the question is purely one concerning " gametic " qualities.

It is submitted that what is known of the physiological and psychological characteristics of animals—especially man—supports the supposition that such variations do occur. The spirit of adventure, physical courage and the general desire for an active life—qualities popularly associated with the male sex—are found in women as in men, while female qualities such as passivity, timidity, etc., can be recognised in men as well as women, although our civilisation strongly favours the sexual segregation of such qualities.

Characteristics of these kinds might well be " gametic " and result from the particular balance struck between the " active " and " passive " types of protoplasm contributed by spermatozoid and egg-cell.

This conception may be stated as follows :—

Certain physiological and psychological qualities which are popularly associated with the sex of the individual (zygote) are in reality common to both sexes. Their development in any individual is not determined by the sex of the individual but depends upon the relative " activity " and " passivity " of the

[1] The factor for " form of apothecium " of a lichen might not influence the morphological form of the isolated algal constituent, yet the algal characteristics might re-act upon the lichen as a whole.

strains of protoplasm which combined to form the individual at fertilization.

Somewhat analogous would be a lichen in which fungal or algal qualities predominated in accordance with the strains of fungus and alga from which the lichen was built up.

Quite apart from these qualities are the factors that determine whether the individual is a male or female. These differences depend, not on the " active"—" passive " balance arrived at between the two portions of protoplasm that unite at fertilization, but probably upon something specific, such as the sex factor or sex chromosome which may be introduced into the zygote by either androplasmic or gynoplasmic gamete.

Sexual reproduction in the higher animals is so specialised that the activities of the individual are inevitably conditioned to some extent by it. Those peculiarities, the nature of which is conditioned by the sex of the individual, form the group of secondary sex characters—in which group there may be in addition other characters whose connection with sex is somewhat obscure. The expression of the former class of gametic qualites may be curtailed to some extent by the limitations imposed by the sex of the individual (*i.e.,* by the secondary sex characters), but the effect of these limitations in masking the gametic qualites has been probably much exaggerated, owing to the undue importance given to the sex activities in civilized societies. The conditions in civilized communities are very largely artificial and the tendency has been to emphasise both real and supposed sex differences in man by tradition, education and limitation of activities.

Where these artificial limitations have been broken through by either sex it becomes more possible to distinguish between the two classes of qualities; and that many of the characteristics ordinarily regarded as sex-associated are in reality independent of sex becomes apparent. A comparative study of other animals confirms this view.

Thus, briefly, there are two groups of characters with which we have to deal. (*a*) The characters referred to as gametic or " active "—" passive ", which depend upon the particular balance struck between the "active " and "passive " types of protoplasm united at fertilization. These are not sex-limited, but may be developed in an almost equal degree in either sex. (*b*) Those which observe the ordinary Mendelian rules of inheritance and

are associated with the sex-chromosomes, *i.e.*, those which determine the kind of spore produced in plants or the sex of the individual in animals. Associated with these are true secondary sex characters, the expression of which in the individual is sex-limited.

Considered from a sociological standpoint, many of the anomalies of our civilization may be regarded as due to treating the former group as though they were subject to more or less complete sex limitation. The desire for personal responsibility and achievement, the pleasurable excitement of running risks, etc., are assumed to be male traits (though the war has, to some extent, modified this view) whereas, from the point of view put forward in this paper, these should be regarded rather as "active" (or androplasmic) characteristics common to individuals of both sexes, the balance varying with the individual but not necessarily being correlated with the sex of the individual.

The desire for a secure and settled mode of life with which a woman is conventionally saddled is no more feminine than is the same desire in a man of the temperament that is happiest in some secure, routine and subordinate employment with little or no responsibility. This is a "passive" or gynoplasmic rather than a feminine characteristic.

May not the feminist movement be regarded as an instinctive and unconscious attempt to separate these gametic characteristics common to the sexes from those showing real sex-limitation? It is to be regretted that the standpoint from which social matters of this kind are discussed is generally political or economic rather than biological.

In discussing the hypotheses that have been put forward here, and in following out the implications arising therefrom, the author has endeavoured, while indicating the width of application, to direct attention for the most part to the simpler cases, in which the issue is usually more clearly defined. In many instances, too, the argument could have been strengthened by the inclusion of additional examples to illustrate or extend the point at issue. It has been thought preferable however to present a short outline for criticism rather than a more elaborate scheme, in order that the main hypothesis may not be obscured by the details.

Throughout the discussion the difficulty has been severely felt of dealing clearly with two quite different series of facts for which, in current usage, the same set of terms is employed. The

confusion is one that arises quite apart from the hypothesis outlined above. The use of *androplasmic* and *gynoplasmic* and of *male* and *female*, etc., to distinguish between the qualities of the gametes and those of the individual ("sporophyte" of higher plants) is an attempt to solve the difficulty and make discussion of the problem possible.

The present paper is, to a large extent, the outcome of discussions with my wife (Dr. M. C. Rayner) and it is not possible to acknowledge too fully the extent to which it is indebted to her helpful and stimulating encouragement and criticism at all stages. At the same time, the writer is prepared to accept full responsibility for the unorthodoxy of many of the views put forward. It is felt that anything that arouses controversy is to the good, whether the ultimate result be to set up new, or establish more clearly the current views.

In conclusion, it is hoped that the fact that the writer is at present engaged in other than academic duties may excuse some of the imperfections of the article.

THE RECONSTRUCTION OF ELEMENTARY BOTANICAL TEACHING.

"THE STUDENT AS A SYNTHESISING ORGANISM."

To the Editor of THE NEW PHYTOLOGIST.

DEAR SIR,

As a student who is trying to arrive in a particular case at some knowledge of the significance of morphological and physiological characters, I have been much interested in the previous correspondence. In my own problem these two sets of characters are so closely interwoven that it is impossible to balance one against the other, and the only sound position seems to me to be that which regards the plant as a whole, as a living organism, living but nevertheless organised.

Until we know the physiology of the plant as completely as we do its morphological organisation there will always be a residual quantity of knowledge which must be taught, if at all, as pure morphology. The physiology which is known seems to me to be inseparably bound up with the organs which carry on such physiological functions. The teaching of all physiology is, therefore, the explanation of the functions of morphological parts, while the teaching of morphology is the explanation of the structures which carry on known functions, with or without the description of structures of which the function is still unknown. An engineer must know what his machinery does and also the parts of the machinery which act, why they act and what each part does, together with the structure necessary for the accomplishment of the function of each part. Botanical students and teachers appear to be in the same position.

The real difficulty in our case seems to me to be the neglect of the psychology of the student by the teacher. Two of your correspondents (NEW PHYTOLOGIST, Vol. XVII, p. 54 and p. 105) have taken proper notice of this factor, and they both plead for freedom. I am in close agreement with both.

A rational solution of the problem can be attained only after an exhaustive treatment of all the known factors. The product of assimilation is a true and accurate knowledge of plants which is capable of application in the various fields of botanical activity; the assimilating organism is the student; the material assimilated

can be divided into two classes, facts and theories; the source of the material varies, it may be plants, books or lecture notes; the synthesising energy is supplied by the teacher.

An assimilating organism is obviously necessary and the proper study of its characteristics is essential to the solution of the problem. That facts are necessary is clear, since without some facts there can be no theories. The necessity of facts can also be demonstrated by placing the organism in an atmosphere devoid of facts; synthesis of effective knowledge does not take place. The necessity of theories can be shown in a similar way by depriving the organism of its supply of this class of material; with facts present and theories absent the former merely accumulate in the outer regions of the organism and, not being assimilated, the material is not effective in so far as it cannot be applied in the various fields of activity.

The four remaining factors are—plants, books, lecture notes and the synthesising energy. That plants are necessary for the life of the organism is clear, since without plants there could be no botanical student. The result of varying the supply of plants must be considered. With a quantity just sufficient for the life of the organism, such as is supplied in city schools and tutorial colleges, the organism becomes stunted and develops malformations. The plant material can be classified as non-available, available and excess. The non-available plant material is necessary because it forms the basis of the available material. The available plant material must not be in excess; if it is not aërated with at least a little theory the process of assimilation is stopped. Such material must, however, be present in abundance as the demand for it by the organism varies greatly from time to time. It is clear, therefore, that the plant material is detrimental only in extreme conditions, and with a normal supply the variations in quantity appear to have little effect on the amount of assimilation.

The book supply is important. If the supply be very small the general health of the organism is affected, but an excess is not detrimental since the organism uses just the amount required for assimilation and life in general, and does not become aware of the presence of a greater supply until the need for such material arises. This is because the book material is of a gaseous or theoretical nature, unlike the plant material which is solid fact.

It is with the two other factors that we are most directly concerned. The lecture note material acts as a limiting factor

within certain limits; even very small quantities may be utilised by the organism and the amount of assimilation varies directly with the supply up to a point where this particular material begins to have a toxic effect on the organism. It is important, therefore, that the supply of this material should be kept below the toxic concentration, which is not very high.

The supply of synthesising energy also acts as a limiting factor but within wider limits. It is, as a rule, present in very small quantity, and the amount of assimilation depends chiefly on this factor. Plants, books and lecture notes are usually present in normal quantity. Assimilation varies directly with the supply of synthesising energy up to a point where the intensity of the energy has a detrimental effect on the organism and tends to burn or shrivel it. This extreme is never reached under natural conditions and occurs only rarely in artificial conditions.

As mentioned above the supply of lecture note material has a toxic effect at a comparatively low concentration, it is clear, therefore, that the synthesising energy is something different in kind. It is supplied by the teacher, and it is or should be the aim of any rearrangement of conditions for the organism to increase the supply of this synthesising energy. We must have teachers who teach because they must tell someone of the many wonderful things they have seen and know, not because the syllabus of a given university contains certain items of fact or theory which must be assimilated in order that the organism may be passed as healthy, after a superficial test by a body of experimentalists who have not as a rule had time to study either the organism or its environment in sufficient detail.

The importance of the supply of synthesising energy acting as a limiting factor cannot be taken too seriously in the present dis-cussion, since it is the factor for which the teacher is directly responsible.

Considering the generation of the energy at its source, it is clear that the radiations will have an illuminating effect only when the enthusiasm of the teacher reaches a red heat, and that the effect will increase as the enthusiasm increases up to white heat. This fact is pointed out by one of your contributors (op. cit. p. 106), and the generation of synthesising energy by enthusiasm is proved by the case he mentions.

The direction of the radiation is another important point; to be effective the radiation must impinge upon the organism.

Here we come to a distinction, not between morphology and physiology but between the morphologist and the physiologist as sources of synthesising energy. The material dealt with by the former is chiefly solid fact, and a very small proportion of the radiation is deflected to criticism of the work of others. In the latter case the material to be classed as fact is frequently not very solid and much of the material dealt with is theory, so that a large proportion of the radiant energy is deflected to the criticism of the work of other teachers, leaving only a small proportion for transmission to the student.

This is unfortunate, but it is a fault inherent in the present unsettled condition of our knowledge of physiology. Such misdirection of energy will remain until the physiologist learns, as the morphologist has done, that although a theory may be wrong the facts upon which it is based may be real facts and, therefore, worthy of careful consideration and incorporation in our current knowledge. This point also explains the relative success of the two schools in their appeal to the student.

In my opinion too many of the recent additions to our knowledge of physiology are regarded as suitable only for advanced students. If the plant as a whole is to be taught to elementary students it will be necessary to incorporate many recent advances in physiology in the elementary course. One must, of course, be more or less dogmatic in elementary teaching, and some recent theories may be disproved within a few years. The facts as such, however, can always be given, and it develops a healthy point of view in the average elementary student when he realises that botanists do not know all there is to know about plants.

In this brief and somewhat superficial analysis of the various factors influencing the assimilation of effective botanical knowledge by the student, no distinction arises between the morphology and physiology of the plant. There may be no magic in words, but I suggest that the desired point of view might be attained if we had no more courses on Morphology, Physiological Anatomy or Physiology and taught instead Organography and Ecology. Organography might occupy the first year of the pass course and would include the essential parts of much that is now taught concerning the morphology, anatomy, physiological anatomy and cytology of all the larger groups of plants, treated from the point of view of causation and function. Ecology might occupy the second year and would include the relation of the plant to its

environment, using environment in its widest sense, and including all the processes connected with the assimilation and utilisation by the plant of food materials, and the reactions in structure and in health of the plant to variations in degree and kind of the supply of these materials. This ecology would include the usual syn-ecology and also aut-ecology, which together with the study of the constitution of the organism should form the basis of any future evolutionary teaching.

It would be possible to conduct an elementary course on similar lines, if, instead of groups of plants, individual species formed the subject of study. The principle of the study of types might be extended and the physiology as well as the morphology and anatomy of the wallflower or sunflower, for example, could be taken from germination to seed-formation, the student sowing the seed and tending and studying the plants at all stages. In this way even an elementary student would be given an opportunity of realising the plant as a living and organised individual.

Yours sincerely,

JAMES SMALL.

BEDFORD COLLEGE,
Regent's Park, N.W.1.
5th June, 1918.

BOTANY AND THE TEACHING OF BIOLOGY.

To the Editor of THE NEW PHYTOLOGIST.

DEAR SIR,

Botanical Bolshevism! If this be indeed an accurate description of the situation, may we not push the simile a little farther and seek to show that just as political Bolshevism arose as a reaction against intolerable conditions in the body politic so botanical Bolshevism has come into existence because it is actually a fact that "all is not well with the position of academic botany in this country," and that "the existing position is not only unsatisfactory but even dangerous." Grave disorders invite desperate remedies! Jesting apart, I feel that botanists generally are greatly indebted to you for initiating a discussion on "The Reconstruction of Elementary Botanical Teaching" in THE NEW PHYTOLOGIST, and for the opportunity which has been afforded to ventilate all aspects of the subject.

The powerful plea for reconstruction along "live lines" can hardly fail to serve a useful purpose, if only the promotion of free discussion and the exchange of views.

It seems significant that those contributors who have most severely criticised the views expressed in the memorandum have frequently based their criticism on a plea for freedom of action.

"Freedom to form a scheme of teaching to meet his (the teacher's) 'own needs.' The right of every botanist to think and practice according to his own beliefs without hindrance." This surely is what is sought also by the original signatories!

After careful study of the memorandum I do not find a denial that it is feasible—even under existing conditions—to arrange an elementary course of Botany which would deal with the plant as a "living organism." I do find many arguments that if this is the case it is done in spite of and not because of existing regulations. Elementary courses are not always in the hands of distinguished and experienced botanists, nor is it the good fortune of all students to attend such courses or to realise the wider point of view at this stage of their work.

I take it that the purpose of the memorandum was not to join issue between the teaching of Morphology and the teaching of Physiology as such, but to plead for the teaching of Botany to the elementary student so that he may acquire a conception of the plant a sa living thing, faced, as is he himself, with the problem of existence in a not too friendly world : some conception also of the extent and constitution of the vegetable kingdom as a whole, and, above all, a true appreciation of the immense significance of the more fundamental aspects of plant metabolism in relation to animal nutrition and the food-supply of the world.

If the teaching of botany is to serve any purpose other than the training of professional botanists ; if it is to play its proper part in bringing home to the student the close interdependance of plant and animal life and the fact that his own life-processes are related to those of plants in the most diverse and intimate ways, then elementary botany must be taught on other lines than those usually prescribed for elementary courses.

It is not only that the morphological bias of elementary syllabuses tends to give the whole subject an aloofness which helps to perpetuate the common attitude that Science is something essentially different and apart from the facts of every day

life, it is that it makes it difficult for any but a most experienced and able lecturer to introduce the student to the study of plants in the light of the more recent as well as the older phases of botanical knowledge.

The plea, as I understand it, is not that plant physiology should replace plant morphology as a basis for elementary teaching because it is a better thing. It is a plea that the student of Botany may have an opportunity of realising at the outset the *general* scope of our existing knowledge of plants, and that the more recent as well as the older aspects of that knowledge may find a place in such a presentation. If this is attempted at present existing Syllabuses usually handicap the teachers, and the handicap is more severe in proportion to his inexperience.

The practical difficulty of teaching plant physiology experimentally to large elementary classes is a very real one and, in my experience, can be only partly met at present by the demonstration of experiments set up by a member of the teaching staff or by selected students. The point of view of the teacher is important if such experiments are to carry their full educational value. Some acquaintance with the practical cultivation of plants should be recognised as an indispensable part of the equipment of the botanist —not only of the plant physiologist and researcher but of the teaching botanist. It is not infrequent in the botanical laboratory to see elementary experiments fail for lack of precautions at which a practical gardener would smile !

Arising out of these remarks there is an aspect of the subject which provides cogent argument for a change in the teaching of elementary Botany on the lines suggested in THE NEW PHYTOLOGIST of December last. Of the students who attend elementary courses in Botany comparatively few will become professional botanists or scientific researchers. Their case seems to me less pressing than that of their fellows since opportunities will necessarily recur in their subsequent botanical training. Such students will gravitate as at present, towards that aspect of the subject which most attracts them and this, as at present, will be determined partly by the cast of their own minds, and partly, may we say—under the fierce light thrown upon this controversy by an earlier contributor —(p. 54) by the charm and persuasiveness of their teachers !

What of the remainder ? Many will become teachers who may or may not deal with Botany as a part of their curricula; large numbers are medical students who will doubtless tend, as at

present, to regard their botanical work as a thing distinct from other departments of biological knowledge and a trivial thing at that ! Others,—and lest the argument should be advanced that the fate of these is not a matter of urgent concern to university teachers, be it noted that their numbers are rapidly increasing in response to the invitation extended them by the universities— are students taking university degrees in Agriculture or in Horticulture.

To students in all these categories it is especially urgent that an Elementary Course of Botany should serve as a general introduction to Biology, and to some of them it may be the only opportunity of acquiring scientifically sound biological ideas.

To quote from a recent volume of essays on " Science and the Nation."

" Let our universities provide courses of scientific instruction or the unscientific as well as the purely professional courses. . . . For the sick have need of a physician."

Let the Elementary Course of Botany be of such a kind that to students of—so-called—applied science it may be made abundantly clear that " what people call applied science is nothing but the application of pure science to particular classes of problems."

If the university teacher of Botany can do this he will not need to rely upon " the subtle and mysterious speculations " of morphology in order to capture the interest of his students nor require to stimulate it, at this stage of their scientific education, by invoking a " semi-religious fascination."

I find myself in general agreement with the practical suggestions made in the original memorandum. It seems to me desirable that, if possible, the elementary course in Botany corresponding with the ordinary Intermediate Science course should be either a two years' course or be of the nature of a double course, one part of which should consist of a general elementary course on the lines laid down, calculated to serve as a general introduction to biology for all classes of students, and the other to be of a more academic kind designed to give the necessary training in technique as well as a more extended detailed knowledge of the essential facts of structure in various plant groups.

The general course would not only lay a wide foundation upon which to build up sound botanical knowledge but it should serve to bring home to the elementary student the significance of the scientific method in general and the meaning and value of research.

With regard to the inclusion of ecology in an elementary course I share the views expressed by "Witness" and by Dr. Jeffreys. The proper place of ecology in elementary work is indicated in the Editorial Note appended to an earlier contribution (p. 53). The problems of plant-ecology demand a wide practical knowledge of systematic botany, a sound knowledge of plant structure and a working knowledge of the methods of the plant physiologist. They constitute in fact applied Botany in the widest sense. The nature of these problems can only be properly appreciated by trained botanists.

We hear much of the neglect of Science. We are told unceasingly that Science does not take its proper place in the life of the nation. It is for botanists to see to it that botanical science is taught so that it carries its full weight as an educational subject; it is for them to make clear that the fundamentals of botanical knowledge should form an indispensable part of the intellectual equipment of every educated person.

It seems to me indisputable that this purpose can be served best by a change in the *spirit* of botanical teaching on the lines suggested by the Memorandum in THE NEW PHYTOLOGIST of December, 1917, and I am glad to take this opportunity of expressing my personal indebtedness to the authors for their lucid analysis of the present situation.

It remains for those botanists who are persuaded that these things are true to show that such a change of spirit can be brought about without any lowering of the high standards which have been set and maintained hitherto in the teaching of academic Botany.

<div align="right">I am, Sir, etc.,</div>

<div align="right">M. C. RAYNER.</div>

AN ARGUMENT FOR MORPHOLOGY.

By M. C. Stopes.

GRANTED that Morphology is the dry bones of the science of Botany—*One does not teach a child to walk or run till the bones of its legs are firm.*

Students come to their teachers full of the hazy golden dreams of youth, dreams which are most easily transmuted into theories, theories audaciously ready to deal with complex and difficult phenomena. Only too readily do theories flourish on but hazily comprehended facts, and the only way even partly to counteract the inherent laziness and sloppiness of the human brain is to train it, while it is still plastic, to deal so far as possible *exactly* with observable phenomena. To do this (in Botany) the external and microscopic morphology and anatomy of plants is the medium for illustration most available for the overburdened teacher of elementary botany. In this study exactitude of observation can be attained without elaborate apparatus, and it can be obtained without the need of "correcting" for all sorts of unknown factors. To cut sections of and draw the cells accurately of definite portions of plant tissue is a sterner mental training, and, because it gives a useful realisation of the essential construction of a plant's body, is a better mental foundation than any amount of "cross breeding" or measurements of transpiration by one who has no exact picture of the tissues he is dealing with. Never shall I forget the ridiculous spectacle an advanced English student who had been only "physiologically" trained, made in a seminar of a German University when he insistently advocated wonderful theories of his own about the flow of water. It was patent to everyone who heard him and knew the mechanism of the plant's body, that the man hadn't the ghost of an idea of the distribution of essential tissues.

With early youth the mind loses any power it ever had of dealing accurately with phenomena, unless in youth it has been given a precisely accurate bent. Later on, if once this rectitude has been established, the mind can be trusted to play on bigger and vaguer or more complex themes. Whatever the after work on plants, an accurate mental picture of the essentials of their organs

and tissues forms the firm foundation of all conceptions about them.

This does not mean that I propose that there should be no physiology in an elementary course, but that it should be subservient to anatomy, microscopic study and morphology, because the last three give the permanent stable bricks and mortar which the first uses. The same bricks can be rebuilt in a thousand different ways, as the students ambitions rise; without any solid bricks his structures and edifices will be flimsy indeed.

In a more elaborate form the elementary course of botany should teach the student this:—Plants, like animals, are an expression of that mysterious, complex, and intricate essence we call life; we can only study (plant) life through its physical presentations in terms of complexes of chemical molecules. These meet our eyes compacted into various cell tissues and organs, of which the construction is specifically stable enough for our crude purposes to look on as fixed and definite. *We must hold on to the definite details we can see and measure to get any firm foundation for our ideas at all.* Life makes these cells and organs as its tools. When we know the details of the material expressions of that fantastically elusive thing called life, we may be able to catch it at some of its dodges, otherwise we will be in a perpetual fog and life will laugh at us. It is doing so probably in any case, but youth is serious and should not be told this.

PALÆOBOTANICAL DEPARTMENT,
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THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.

By James Small, M.Sc. (Lond.), Ph.C.

Chapter IX.

FRUIT DISPERSAL IN THE COMPOSITÆ.

ALTHOUGH there is a considerable variety of fruits in the family which are dispersed by animals, the chief dispersal mechanism is the pappus. The structure and evolution of this organ is dealt with in Chap. V. Its efficiency as a dispersal mechanism has been questioned by a number of observers and experimenters ; it was considered necessary, therefore, to investigate the problem experimentally, and the method and results are given in Section B of the present chapter, after the brief account of previous records in Section A. As the experimental results are somewhat at variance with accepted views the hydrodynamics of the simplest case are discussed in Section C. The bearing of the results on the problem of the development of the family is indicated in the last section of the chapter.

A. History.

The dispersal of seeds and fruits has been the subject of many observations. The literature of the subject was dealt with by Hildebrand (V, 32), and again by Hemsley (23). A further index of the literature from 1873 to 1890 is given by MacLeod (27), and a more recent bibliography by Sernander (33), who refers to Linné's *Oratio de telluris habitabilis incremento* of 1743 as the beginning of the study of plant dispersal. As there is a readily available account of the general phenomena with a good bibliography by Praeger (30) only special points will be mentioned.

Cassini (8) was one of the first to consider fruit dispersal in the Compositæ, and he differentiated eight methods by which the fruits are liberated from the capitulum. De Candolle (11) gave details of many species, and pointed out that many wide-spread species have no pappus. He formed the opinion that the pappus was effective as a means of dispersal for short distances only, *i.e.*, up to half-a-mile. Hildebrand (V, 30) considered the various modifications in the fruit in relation to their dispersal, and gave examples from the Compositæ in his general treatise, and also in a previous account of hooked fruits (V, 31). Bentham gave a short

general account (I, 7, p. 572), but laid great stress on the colonising powers of the Compositæ apart from their dispersal mechanisms. Wallace (41) explains the anomalous distribution of certain Compositæ by their "great powers of dispersal," and in Chap. XXIII gives some detail of the general migration from north to south along the mountain ranges. More recent observations by Guppy (21-22) and Praeger (30) emphasise the importance of ocean currents and birds as means of dispersal.

A curious point is raised in the consideration of the dispersal of the radiate variety of *Senecio vulgaris*. Professor Trow informs me that although it is possible that the radiate character was introduced into Great Britain from the Channel Islands it would be more correct to speak of the spread of the character "radiate" than of the radiate variety. The records of radiate groundsels are records of the character but are not necessarily records of the same variety.

Dispersal by Animals.

Dispersal by birds for comparatively long distances is given by Darwin (II, 16), Wallace (41), Hemsley (23), Guppy (21), Praeger (30) and others. The fruits during dispersal may be either inside the bird (in the crop or elsewhere) or outside the bird amongst its feathers or among the mud which occasionally adheres to the feet.

Adherence of the fruit may be obtained by glandular structures, as in *Adenostemma*, *Siegesbeckia* and *Wulffia* (V, 30; IV, 98) or by mucilaginous pericarps, as in *Rutidosis* (V, 14), *Chrysanthemum Fontanesii*, *Ruckeria* and *Trichocline* (V, 32), and also in *Chrysanthemum multicaule* as observed by the writer. Adherence may be obtained also by hooks, as in many genera ; the hooks being on the involucre, as in *Arctium* and *Xanthium*, or on the pappus, as in *Bidens*. These cases and several others are mentioned by De Candolle (11), Hildebrand (V, 30-32), Kronfeld (VII, 3), Huth (V, 41) and others.

Dispersal by man has been mentioned only in passing by most botanists, but is the subject of a paper by Thellung (34) who mentions a number of Compositæ which have been dispersed as weeds or as horticultural plants. This rather neglected branch of fruit dispersal is most interesting on account of the many traditions with which it is connected, such as the reputed introduction of "Stinking Willie" (*Senecio Jacobæa*) into Scotland in the fodder of the German cavalry used by William, Duke of

Cumberland. Such material is, however, pabulum for the philologist and archæologist rather than the botanist.

Dispersal by Water.

Among the first observations of fruit dispersal in the Compositæ is a series of experiments by Hoffmann (24) on the floating powers of a number of species, most of which sank within twenty days. De Candolle (11) and Hemsley (23) give rivers and ocean currents as agents which disperse fruits to great distances, but no case of such dispersal in the Compositæ is quoted, although dispersal on floating logs and icebergs, as mentioned by Darwin (11, 16) and Guppy (22), is quite possible. Kronfeld (VII, 3) showed that pappus fruits such as those of the dandelion floated much longer with the pappus attached, even when it is closed. The closed pappus usually surrounds an air bubble which assists in the flotation.

In the case of Krakatau (15) some of the species of *Wedelia* and possibly also those of *Conyza* and *Blumea* were transported by ocean currents, and in the somewhat similar case of Taal Volcano (19-20) *Wedelia biflora* and *Eclipta alba* most probably arrived by water. The latest addition to the meagre list of water-dispersed Compositæ is *Ambrosia crithmifolia*, which is given by Guppy (22) as transported on drifting logs.

Dispersal by Wind.

The pappus has usually been regarded as an efficient mechanism for dispersal by wind, and there have been many general observations of the structure on this account, such as those of Hildebrand (V, 30-32), who also mentions cases (V, 30) of wind dispersal of the whole capitulum where the involucral bracts act as wings. Kronfeld (VII, 3) considered that in the case of *Tragopogon pratensis* the lateral cilia of the setæ produce a structure which acts as if it were a continuous membrane. Taliew (V, 65), Steinbrinck (V, 64), Hirsch (V, 33), Frieb (18) and others have noted the biological significance of the hygroscopic movements of the setæ and involucral bracts, dispersal being favoured by dry winds and prevented by moist winds.

Foerste (17) mentions a curious addition to the dispersal mechanism in *Ambrosia trifida.* The achenes are beaked, with five short protuberances at the base, and five or six strands of ice have been observed attached to these on frosty mornings: as these " ice-curls" were 1½ to 3 inches long Foerste suggests that they aid

the wind dispersal of the fruits. Another curious but better known anomaly is the dispersal mechanism of *Parthenium hysterophorus*. Here the bracts enclosing two male florets are attached to the top of the achene of each female floret, and these bracts with the withered male florets enclosed act as wings.

The mechanics of the pappus have been considered by Dingler (12), Praeger (30), Mattei (28) and Dandeno (9), who all regard the mechanism as a simple parachute.

Apart from these general observations there is the controversial question of the distance to which a pappose fruit can be dispersed by the wind. De Candolle (11), although he regarded the wind as " la cause la plus générale et la plus ordinaire de dissémination des espèces sur toute la surface d'un pays," maintained that there was no evidence for the transportation of seeds over even narrow arms of the sea. He was, moreover, sceptical about the records of grains of sand, etc., being blown for long distances by the wind. Bentham (I, 7) also considered that a few miles was the limit for the dispersal of pappose fruits even by strong winds. Kerner (25), and more recently Beauverd (1), have shown that in the Alps pappose fruits are raised to a considerable height, but they both consider that all such fruits fall when the upward current fails in the evening, and that they come to rest very close to their starting point.

Praeger (30), with whom Guppy (22) agrees, calculates from the rate of fall in quiet air that many pappose fruits would require an initial elevation of about one mile before they could be blown to a distance of fifty miles by a wind of 50 m.p.h. Heavier fruits would require a still greater elevation according to Praeger. Willis, although he states (IV, 94) that the Orchids and Compositæ are best suited for long distance dispersal, and considers that wind-carried seeds arrive more frequently than other Angiosperms on hill-tops, maintains as a result of his observations on hill-top floras (43-45) that such cases of long distance dispersal are rare even in the Composite, and that " we have little evidence to show that it occurs for instance between one continent and another."

In spite of the objection of lack of evidence for long distance dispersal which is raised repeatedly by the above-mentioned authors, the positive evidence for such dispersal makes a longer list, and has secured more adherents than the view of the opposition. Wallace, for instance, in his " Island Life " says, " we are as

sure that seeds must be carried to great distances as if we had seen them so carried," and he furnishes a very good argument against the negative observations of De Candolle (who relied chiefly on the statements of the sailors that they had seen insects but not seeds blown long distances out to sea), and Kerner (who examined some part of the surface of a glacier but found no seeds other than local species). Wallace points out that if " every year a million seeds were brought by the wind to the British Isles from the continent, this would be only ten to a square mile, and the observation of a life-time might never detect one ; yet a hundredth part of this number would serve in a few centuries to stock an island like Britain with a great variety of continental plants." He also notes that the arrival of seeds and colonisation are different matters ; seeds arriving on ground already fully occupied would require more than a wind-dispersal mechanism to enable them to compete successfully with the established inhabitants.

Beccari (2) gives evidence for the dispersal of seeds for distances of 1000-2000 miles, *e.g.*, *Nepenthes ampullaria* from Ceylon to the Seychelles, but does not mention any special Compositæ. Similarly Engler (14) gives fourteen species of Angiosperms as transported by wind to the Sandwich Islands, but excludes the Compositæ on account of the width of sea to be crossed. Warming (42) also supports wind-dispersal to a distance of at least sixteen miles for quite heavy fruits. The distance is increased by Vogler's observations (38-40), but this author points out that, although wind-dispersal of seeds is possible up to 100 kilometres, more importance is to be attached to such dispersal for 3-20 kilometres and to the possibility of dispersal over high mountain ranges. Kronfeld (26) considers the rapid dispersal of various introduced Composites to be due to the efficiency of the pappus. Ridley (31) also considers that plumed fruits " can at least occasionally cross successfully large areas of sea," but points out that dense forests present an obstacle to the free dispersal of pappose fruits. Further confirmation of the efficiency of the pappus is given by Bessey (6). Schimper (32, p. 80), after giving the views of De Candolle and Kerner, quotes the case of Krakatau as evidence of wind-dispersal for twenty miles over the sea, and considers that " the significance of anemophilous means of dispersal in relation to the origin of an insular flora has been finally determined by Treub's important observations."

The case of Krakatau is of special, interest since of the eight

angiospermous species found by Treub (36) in the interior of the island and not on the strand three years after the eruption four species were Composites : *Wollastonia* (=*Wedelia*) sp., *Conyza augustifolia*, *C. indica* and an unidentified species of *Senecio*. In the absence of other evidence it is at least possible that this " *Senecio* " of Treub was *Emilia sonchifolia*, which is very like a *Senecio*, and which was found by Penzig (29). No *Senecio* was found by either Penzig or Ernst (15). The former found five and the latter eight Compositæ, of which *Blumea balsamifera* and *Vernonia cinerea* were found by both and *Emilia sonchifolia* only by Penzig in 1897, fourteen years after the eruption.

These three species are particularly interesting as they occur again in the list of ten species of Compositæ found by Gates (19) on Taal Island (in Bombon Lake, Luzon) about three years after an eruption there which denuded the island of vegetation. The re-vegetation was naturally more rapid than on Krakatau as the source of the seeds was about 6 km. instead of about 18 km. distant. In both cases a number of Composites were strand plants, evidently dispersed by ocean currents, but on Krakatau four species of Compositæ were undoubtedly transported by the wind, and at least seven species on Taal were probably wind-borne, two (*Blumea* sp. and *Pterocaulon cylindrostachyum*) occurring only on the crests of mountain ridges and the other five elsewhere in the interior.

The evidence from Krakatau is, therefore, confirmed by the observations on Taal Island, and there remains no doubt whatever of the usual dispersal by wind of a number of Compositæ to distances of 4-20 miles and the occasional dispersal of pappose fruits to distances of over 100 miles.

B. Experimental Wind-Dispersal.

There is apparently no record in which wind of a known velocity has been used in the experimental dispersal of pappose fruits ; all the experiments have been done on the rate of fall in quiet air. It is, therefore, considered advisable to give some details of the apparatus and method used in the present investigation. The apparatus and method were demonstrated to Sect. K of the British Association in 1916, and to the Linnean Society in the same year (33a).

Apparatus.

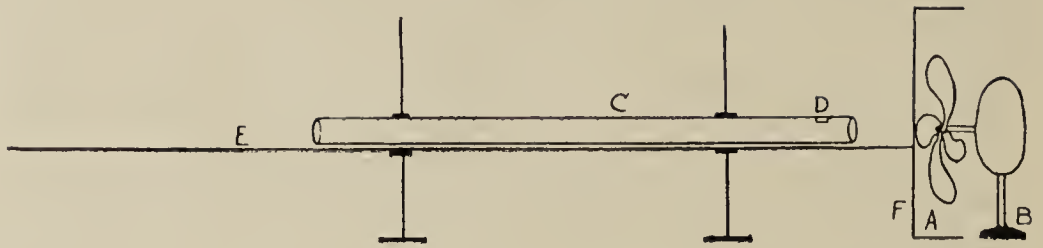The source of the wind was an electric fan (Fig. 25, A)

FIG. 25. Wind Dispersal Apparatus.

attached to a small motor B; by means of different resistances the speed of the fan could be varied. In the results given below Speed 1 is the slowest and Speed 4 the fastest. A wooden guard F, covered on one side with a net, surrounded the fan.

The fruits were blown through a glass tube C. As it was found that the wind eddied at the near end of the tube, a hole D, 2 cms. long and 1 cm. wide, was cut in the tube at a distance of 5 cms. from the end; through this hole fruits were dropped. As the whole length of the tube was 132 cms., this gave 125 cms. as the length for dispersal. A two-meter rule E was used, but as it was placed against the net 3·5 cms. were added to the readings to get the distance from the boss of the fan. This accounts for the constant occurrence of this number in the figures given below.

Anemometer.—The wind pressure was measured by means of an anemometer designed for the purpose. The ordinary rotating anemometer is empirical and not accurate for slow speeds (cp. 7), and further it was more important to obtain a measure of the pressure of the wind on a surface somewhat similar to that of the pappus than to obtain an empirical measure of the velocity of the air moving through the tube.

The anemometer (see Fig. 26) consists of a thin circular disc of tin A against which the wind impinges. The disc is accurately balanced by a ball of solder B on the other end of the top of the T beam. The horizontal part C of the beam is a thin steel rod, soldered to a flat strip of tin which forms the vertical part D of the T. At the base of D are a needle indicator E and a small hook F. The whole of the T beam is accurately balanced by means of solder on the back of D, so that when balanced on the watch-wheel fixed to D at G it remains in any position in which it is placed. In the instrument this T beam is balanced by the steel axis of the watch-wheel on adjustable agate edges at H and K. It is therefore free to move in any direction with a negligble friction when acted upon by a small force.
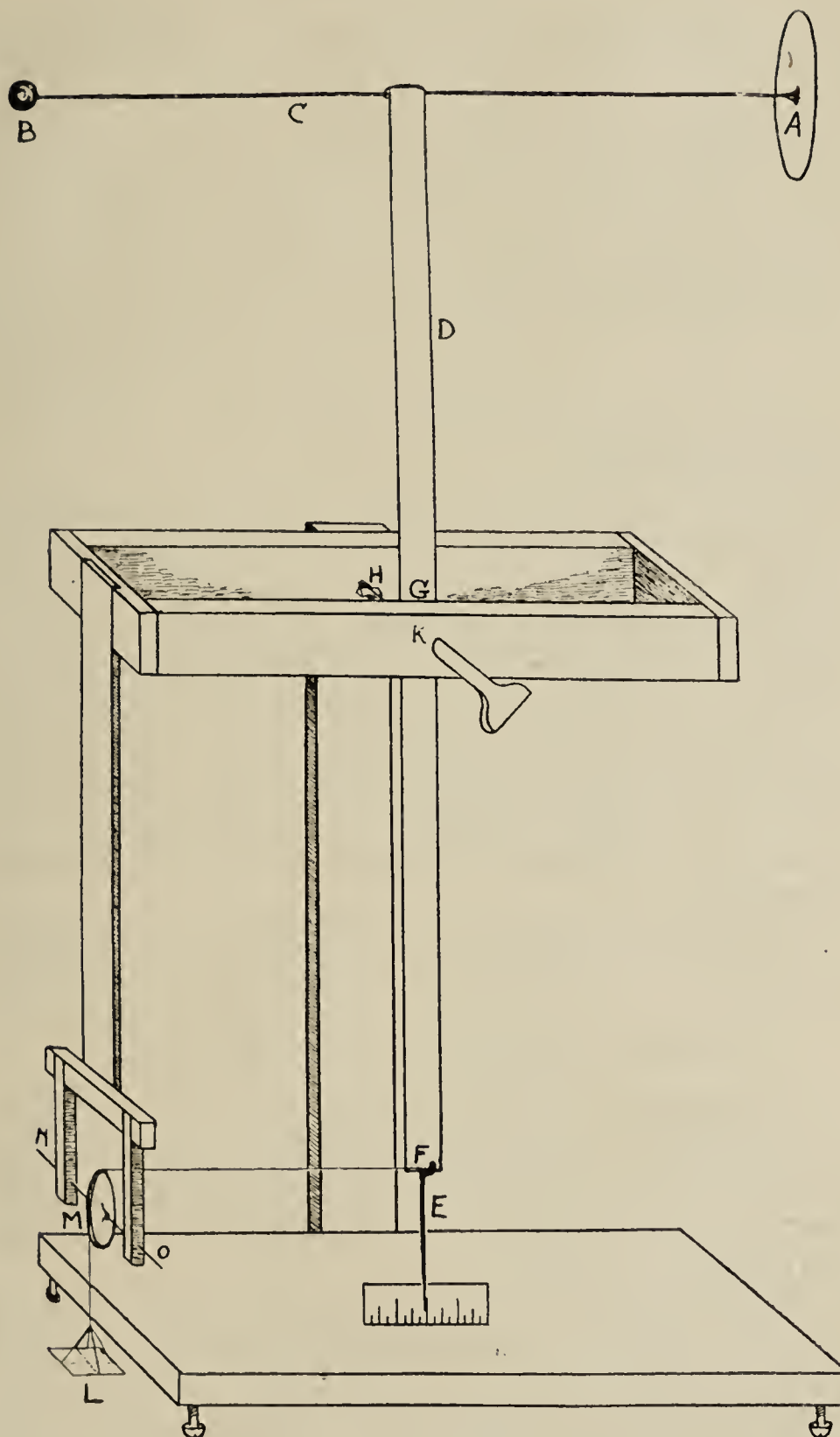
FIG. 26. ·The Anemometer.

The pressure of the wind on A is balanced by weights placed on a scale pan L. The scale pan is a small glass microscope cover-slip, hung by thread over a pulley M ; the thread is attached to the

hook F. The whole apparatus then acts as a simple mechanical couple. The hook F is the same distance from the fulcrum G as the top of the T beam, so that the weight on the scale pan and the weight of the thread, together with that of the scale pan itself, give a direct measure of the total pressure on the disc A. The pulley M has practically no friction, being a small brass wheel running on steel needle points. These needles N and O are adjustable, and when in proper condition the wheel runs for quite half a minute with no sound when given a slight touch. This practically frictionless pulley and the axis at G, which is balanced on sharp agate edges, are the only two points at which friction might cause an error.

When in use with the tube the disc of the anemometer was inserted a short distance into the tube, and as the diameter of the disc is 3·3 cms., and that of the tube is 4·5 cms., the conditions were very similar to those under which the fruits were acted upon by the wind. The almost complete absence of friction and the accuracy of the instrument are both proved by the fact that in a wind sufficient to balance the weight of the scale pan and thread the placing of a weight of ·01 gms. on the scale pan brings the beam as far out of the vertical as the construction of the stand will allow. An accuracy of ·001 gms. is certainly not too much to claim for the instrument.

The smallest weight which it is possible to use is ·16 gms., this being the weight of the scale pan and its suspending thread.

Structure and Properties of the Wind Used.

The strength of the wind produced by the fan varied with the four speeds as above mentioned, and the strength of the wind entering the tube could be controlled further by moving the tube away from or towards the fan. The tube was kept carefully aligned with the centre of the fan.

Smoke was passed through the tube and no marked rotatory movement was observed; the smoke passed straight through, never twisting through an angle of more than 90°. Close to the inside surface of the tube it was retarded and continued to come out for some time after the central mass had passed. The region of retardation was very narrow compared with the width of the tube. It is clear, therefore, that the wind is more or less horizontal with a straight movement through the tube.

The structure of the wind was further investigated by means

of the anemometer, and it was found that there was a hollow cone of relative calm near the centre of the fan with Speed 4; this cone extended about 10-15 cms. from the boss of the fan. Beyond 20 cms. the wind had a steady horizontal pressure, and with lower speeds no cone of calm could be detected.

It was further found that the pressure of wind in the tube at the end furthest from the fan was practically the same as the pressure obtained without the tube and with the anemometer 130 cms. nearer the fan.

As it was not possible to measure all the variations of pressure obtained the relation of the pressure of the wind to the distance from the fan was examined. A series of measurements of the pressure with the tube at various distances from the fan showed that within the limits of the experiments the pressure of the wind, except for Speed 4, varied approximately inversely as the distance of the near end of the tube from the fan. The measurements and ratios are given in Table IX. It is possible, therefore, to calculate from a few measurements the pressure at any given distance.

TABLE IX.

Speeds of Fan.	Distance of Tube	Pressure on Disc as measured.	Ratios
Speed 1.	26·5 cms.	·18 gms.	1·0 : 1·125
,,	30·5 ,,	·16 ,,	1·150 : 1·0
Speed 2.	29·5 cms,	·36 gms.	1·0 : 2.25
,,	44·5 ,,	·26 ,,	1·5 : 1.6
,,	75·5 ,,	·16 ,,	2·5 : 1·0
Speed 3.	26·5 cms.	·56 gms.	1·0 : 3·5
,,	40·5 ,,	·36 ,,	1·5 : 2·25
,,	63 5 ,,	·26 ,,	2.4 : 1·6
,,	103·5 ,,	·16 ,,	3·9 : 1·0
Speed 4.	28·5 cms.	·50 gms.	1·0 : 3·1
,,	87·5 ,,	·25 ,,	3·0 : 1·6
,,	144·5 ,,	·16 ,,	5·0 : 1·0

Since within the limits of the experiments P$=$kV, where P is the pressure, V the velocity and k a constant, V$=\dfrac{P}{k}$. The constant k in these experiments is taken as ·0025 gms., which is the pressure on one sq. cm. of a wind with a velocity of one m.p.h.[1]

[1] This is calculated from the constant given by Berget (4), velocity of 1 metre per second$=$pressure of 125 gms. per sq, metre. This figure is also approximately the same as the theoretical pressure calculated from the density of the air.

In this way the velocity of the wind used in each experiment can be calculated from the pressure such a wind has upon the disc of the anemometer.

Constants—

    Diameter of Tube=4·5 cms.
    Length of Tube for Dispersal=125 cms.
    Area of Disc of Anemometer=8·55 sq. cms.
    k=·0025 gms.

Method.

The essence of the experiments lies in dropping the fruits through the hole D in the tube and determining the maximum amount of wind which has no effect on the fruit when it has once fallen, and also the minimum amount of wind which blows the fruit right through the tube. Preliminary experiments showed that the relative humidity of the air had an effect on the results, so that the R.H. was determined at the time of each set of observations. As the general phenomena are very similar for each species one example will now be given in detail.

Taraxacum officinale, Weber.—The same fruit, an average one, was used throughout the experiment. It was manipulated with tweezers and inserted through the hole into the tube. Two or three observations were taken with the tube at each of the several distances from the fan, the distance being measured from the heavy end of the fruit in each case. The results are given in Table X. The Relative Humidity was ·77; the pappus spread out to form a flat disc-like surface by means of a pulvinus of the *Lactuca* type (see Chap. V, A). The lowest speed of the fan was used throughout the experiment.

In Table X the first column gives the distance from the fan of the near end of the tube. From these measurements the pressure on the disc is calculated from the observed pressure of ·16 gms. at 30·5 cms. (cp. Table IX); this pressure is given in gms. per sq. cm. in the third column. The velocities calculated from the observed pressure, taking k=·0025 gms. in the formula $V=\dfrac{P}{k}$, are given in the fourth column. These figures are calculated to the second decimal place, but under the conditions of the experiment the accuracy of the results is scarcely of that degree. The main point is that they are very much less than would be the case if the mechanics were simply those of a body falling in quiet air,

TABLE X.

Distance of tube from fan.	Distance fruit was blown.	Pressure on disc in gms. per sq. cm.	Velocity equivalent in m.p.h.
13·5 cms.	out immediately.	·0422	4·11
23·5 ,,	,, ,,	·0242	3·11
33·5 ,,	,, ,,	·0168	2·59
43·5 ,,	,, ,,	·0132	2·29
53 5 ,,	,, ,,	·0107*	2.06
63·5 ,,	out, touched.	·0090	1·84
73·5 ,,	,, ,,	·0078	1·76
83·5 ,,	,, ,,	·0068	1·64
93·5 ,,	out slowly.	·0061	1·56
103·5 ,,	out, more slowly.	·0055	1·48
113·5 ,,	39-72 cms.	·0051	1·42
123·5 ,,	24-30 ,,	·0046	1·35
133·5 ,,	18-30 ,.	·0043	1·31
143·5 ,,	17-22 ,,	·0040	1·26
153·5 ,,	15-18 ,,	·0037	1·21
163·5 ,,	11-13 ,,	·0035	1·18
173 5 ,,	9-14 ,,	·0033	1·14
183·5 ,,	5-7 ,,	·0031	1·11
193·5 ,,	5-9 ,,	·0029	1·07
203·5 ,,	4-6 ,,	·0028	1·05
213·5 ,,	3-4 ,,	·0026*	1·01
223·5 ,,	2-3 ,,	·0025	1·00
233·5 ,,	2 4 ,,	·0024	·98
243·5 ,,	0-4 ,,	·0023	·95
253·5 ,,	0-3 ,,	·0022	·93
263·5 ,,	1-3 ,,	·0021	·91

Table X.   Observations on Fruit Dispersal of TARAXACUM OFFICINALE. *For explanation see text.*

Between the point at which the fruit was blown through the tube with no stop whatever and the point at which the fruit was not moved when once it had fallen there was an interesting transition region from 63·5 cms. to 173·5 cms. in which the fruit was blown along in jumps.

Up to 53·5 cms. the fruit was blown straight through, and as far as could be seen did not touch the tube at all. From 63·5 cms. to 103·5 cms. the fruit was blown along trailing with its tip just touching the tube or in a few long jumps. There was sometimes a distinct interval between the jumps, during which the fruit remained lying quite still or showed only feeble signs of movement. This period of rest indicates slight changes in the pressure of the wind, but these were so slight that they are for the present negligible.

The time taken by the fruit to reach the end of the tube increased considerably from 93·5 cm. to 103·5 cms., and after that only five minutes were allowed to elapse between inserting the

fruit and taking the reading. From 113·5 cms. to 173·5 cms. the jumps decreased in length, and after 213·5 cms. the fruit lay where it fell with no further movement.

As the rate of fall in quiet air is about 1 m.p.h. and the wind after 173·5 cms. is about 1 m.p.h. the fruit would be carried a distance equal to that of the fall, if the wind had no other effect than that claimed by Praeger. The diameter of the tube is 4·5 cms. and the length of the fruit about 1 cm., so that the distance of the fall is about 3·5 cms. It will be noticed in Table X that 203·5 cms. is the last point at which the fruit is carried to a distance which is greater than the diameter of the tube. The next reading gives a distance of 3·4 cms., and at this point it can be assumed that the fruit falls as it would in quiet air. There is considerable irregularity in the readings when the wind falls below 1·2 m.p.h. and all that is claimed as really accurate is that a wind of more than 1·01 m.p.h. blows the fruit further than it would do if it had only the effect of mass transport at the speed of the wind as suggested by previous investigators. Below 1·01 m.p.h. the distance travelled by the fruit varied from 0 to 4 cms.

The two points to which particular attention has been paid are :—

1. The least wind-pressure necessary to blow the fruits right through the tube with no stop and without the fruit touching the tube in any way ; this is referred to as the critical pressure A.

2. The highest wind-pressure which could be used without moving the fruit once it had fallen ; this is referred to as the critical pressure B.

These two points are marked in Table X at ·0107 gms. per sq. cm. and ·0026 gms. per sq. cm., and their significance is discussed in Section C. Other fruits are examined more or less in the same way, and the results are summarised below.

Senecio vulgaris, L. Material collected in the open; the R.H. was ·77.

Critical Pressure A—·0055 gms. per sq. cm. 1·48 m.p.h.
Critical Pressure B—·0035   „   „   1·18 „

Senecio vulgaris, L., var. *radiatus erectus*, Trow.—Authentic material for which I am indebted to Professor A. H. Trow. It was found that whereas the pappus remained expanded in the air after being dried in a warm tube with the R.H. as high as ·75, it closed at once when taken out of the tube with the R.H. ·80. Several

fruits were used, and it was found that between ·66 and ·73 the relative humidity had no effect on the wind-pressure required.

Critical Pressure A—·0078 gms. per sq. cm.   1·76 m.p.h.

Critical Pressure B—·0046   „   „   1·35 „

It will be noticed that in both cases the figures are higher than those for the previous material. The fruits were plumper in the variety, but the pappus had about the same development in each. The pulvinus in these two cases is the *Lactuca* type ; the pappus hairs are setose-scabrid as in the dandelion, but the pappus is sessile, not stipitate as in the latter fruit, and spreads at an angle of about 45° with the axis of the fruit, not at right angles to give a flat surface as in *Taraxacum*.

Tussilago Farfara, L.—This was taken as an example of the simple setose pappus with a *Tussilago* type of spreading (see Chap. V, A). As most of the 'fruits' are sterile with empty pericarps care was taken to choose mature fertile fruits, which were obtained in the open. The pappus was too large for the hole in the tube, so the fruit was inserted to a distance of 6 cm. before being liberated. With the R.H. ·78 or below drying was unnecessary as the pappus expanded spontaneously under these conditions.

Critical Pressure A—·00087 gms. per sq. cm.   ·59 m.p.h,

Critical Pressure B—·00081   „   „   ·57 „

It will be noted that the two critical points are very close together. The behaviour of the coltsfoot fruit was peculiar. So slight is the wind necessary for its dispersal that persons walking along the room made sufficient wind to blow the fruit right through the tube. Special care was taken, therefore, to carry on the experiment on a still day with no one moving in the room at the time of the reading,

It was found that with the fan at the lowest speed, and the tube 658·5 cms. away, the fruit was blown right through the tube sometimes with, sometimes without, pauses. At a distance of 703·5 cms. the fruit remained motionless for about five minutes and then moved a distance of 5–40 cms. The critical pressure B is therefore too high, but it was not possible at the time to carry the experiment further, as a complete absence of external currents of air is necessary for the accurate determination of the constant in this case.

Centaurea imperialis, Hausskn.—This was taken as an example of a heavy fruit with a pappus of numerous paleaceous setæ. The spreading of the pappus is accomplished by means of a pulvinus to each seta, the *Cirsium* type of Taliew (see Chap. V, A). As

mentioned previously (Chap. V, A) the pappus is sensitive to a difference of ·03 in the R.H., opening spontaneously at R.H. ·75 and closing at R.H. ·78 when opened by artificial drying. The third speed of the fan was used.

Critical Pressure A—·1318 gms. per sq. cm.   7·2 m.p.h.
Critical Pressure B—·0232   ,,   ,,   3·0   ,,

Ursinia speciosa, D.C.—This was taken as an example of a fruit with a distinctly paleaceous pappus. The fruit has a small tuft of hairs at the base and five, well developed, white and gold plumoso-paleaceous scales at the top. The fruit is not particularly heavy, but the pappus is relatively solid, and its weight is somewhat of the same magnitude as that of the fruit itself, not, as in the other cases, very much smaller than that of the whole structure. The spreading of the pappus seems to be more or less permanent in this case, and no pulvinus could be detected. The third speed of the fan was used.

Critical Pressure A—·0514 gms. per sq. cm.   4·5 m.p.h.
Critical Pressure B—·0118   ,,   ,,   2·1   ,,

Leontopodium alpinum, Cass.—The fruit in this case is small and more or less spherical with no pappus. The average diameter of the fruit is about ·25 mm. The small size of the fruit prevented accurate measurements with the apparatus as arranged. With the tube at 33·5 cms. and the fan at Speed 4 six fruits were dropped through the hole. This was repeated three times with the result that about half the fruits were blown right through the tube, and the others were blown a distance which varied from 35 cms. to 90 cms. The critical pressure A is, therefore, about ·050 gms. per sq. cm., equivalent to 4·4 m.p.h. Six fruits were dropped through the hole with the tube at 33·5 cms. and the fan at Speed 1. Three of them were blown about 5 cms. and the others were lost. The critical pressure B is, therefore, not more than ·0168 gms. per. sq. cm., equivalent to not more than 2·59 m.p.h.

C.   Hydrodynamics of Wind-Dispersal.

According to the views of Dingler and Praeger the dandelion fruit, which falls in quiet air at the rate of ·98 m.p.h., would require an uniform wind of about 50 m.p.h. and an initial elevation of about one mile in order to be transported about 50 miles. or 1 cm. elevation for 50 cms. dispersal. In other words the ratio $\dfrac{\text{distance travelled}}{\text{initial elevation}}$ is a measure of the velocity of the wind required.

In the apparatus described above the initial elevation is at most 4·5 cms. (the diameter of the tube) and thè maximum distance travelled can be taken as the length of the tube, 125 cms. The wind-velocity necessary for the transport of the dandelion fruit to the end of the tube would then be $\frac{125}{4\cdot5}$=28 m.p.h. approx. The experimental result, as shown in Section B, is 2·06 m.p.h. approx. This discrepancy requires some explanation and the essential point lies in the fact that the wind-dispersal of pappose fruits has been regarded hitherto as a hydrostatic problem and not as the hydrodynamic problem which it undoubtedly is. The average pappose fruit is more akin to an aeroplane or a kite than to a parachute or balloon. An aeroplane has a much greater rate of fall in quiet air than a dandelion fruit but a wind of 60 m.p.h. is sufficient to keep the former in the air indefinitely. It must also be noted that as long as the "air speed" is 60 m.p.h. aŋ aeroplane remains up, so that in a wind of 90 m.p.h. an aeroplane could actually drift backwards at the rate of 30 m.p.h. in relation to the earth. This case is somewhat similar to that of the pappose fruit (see below); there would be a considerable element of danger in the above-mentioned stunt but I am assured by aeronauts that it is possible.

Hydrodynamics of Fruit-Dispersal in TARAXACUM OFFICINALE.

The dandelion fruit is taken as the simplest example. Here the main weight of the fruit is at the base of the slender stalk, while at the top of the stalk there are the numerous hairs of the pappus which spread out when the R.H. of the air is ·77 or less. These hairs form a flat, circular surface at right angles to the main axis of the fruit; the centre of gravity is low, so that the structure is that of a simple parachute and is relatively stable.

Now if the fruit is considered to be vertical at first (Fig. 27, A) and a wind with a velocity which develops a pressure M impinges on the fruit in such a position, the pappus being lighter than the heavy fruit body, the fruit does not remain erect. The pappus is acted upon more strongly and is blown ahead of the fruit body, so that the whole fruit becomes tilted as in Fig. 27, B. Once this position is reached the force M can be resolved into two components S and R, S being parallel with the surface of the pappus and R at right angles to that surface. The two components are equal to M $\sin\theta$ and M $\cos\theta$ respectively, θ being the angle of the

axis of the fruit with the horizontal (see Fig. 27, B). The tangential component S is known in kite dynamics as surface slip and is usually considered negligible.
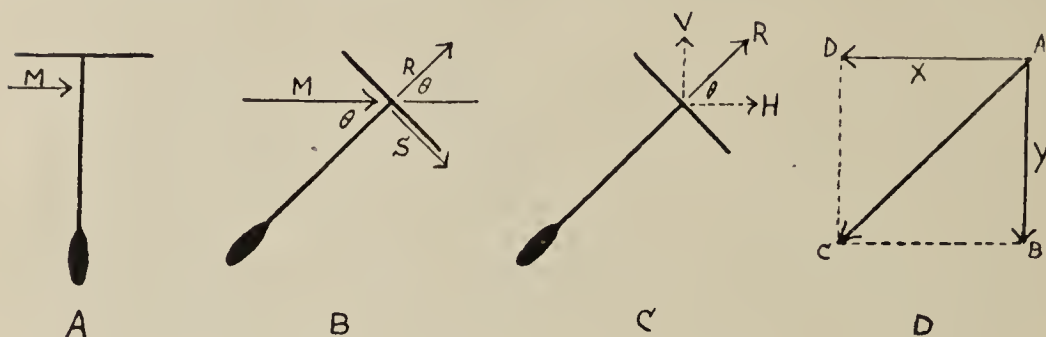
FIG. 27.   Resolution of Forces (for explanation see text).

The Vertical Component.—The normal component R can be resolved further into two components (Fig.27,C) a vertical component V and a horizontal component H.   The vertical component V is equal to $R \sin\theta$ and the horizontal component H to $R \cos\theta$. Since $R = M \cos\theta$, $R \sin\theta = M \cos\theta \sin\theta$, therefore $V = M \cos\theta \sin\theta$. If the pappus surface were a continuous membrane or acted as a continuous membrane (of the area occupied by the hairs and the interspaces) and if the wind were just sufficient to keep the movement of the fruit horizontal the vertical component would be equal to the mass of the fruit.   As the pappus is not a continuous membrane the minimum pressure on the area of the circle of the pappus surface may be greater than the weight of the fruit.   This minimum pressure is described below as the critical vertical component, which is of course a pressure, not a velocity.

The Horizontal Component.   The horizontal component is equal to $R \cos\theta$, which is equal to $M (\cos\theta)^2$.

Surface Slip.   The component S can be resolved into a horizontal and a downward vertical component.   These will be equal to $x S \sin\theta$ and $x S \cos\theta$ respectively; where x is a small fraction.   The close similarity of the experimental and the calculated results (see Table XI) shows, that x is so small that S can be neglected.

Data.

For any further consideration various data are necessary and these have been obtained.

Weight of the Fruit. Bessey (5) gives ·00044 gms as the weight of the dandelion fruit but it was considered necessary to determine the weight of the fruits actually used.   One hundred whole fruits were weighed carefully.

Wt. of 100 fruits=·0756 gms.

∴ average weight of one fruit=·000756 gms.

This is of the same magnitude as Bessey's figure and the difference is possibly due to the fact that the fruits used were very well developed.

Area of Pappus Surface. The constant referred to by this name is not the sum of the areas of the exposed surfaces of the hairs as calculated by Dandeno (9) but the area covered by a circle with a diameter equal to twice the length of a pappus hair. The pappus from eight fruits was stuck to paper and measured under a dissecting microscope. The longest hairs and the mass of hairs were both measured.

Diameter in mm. as measured by the longest pappus hairs= 12·5, 12·0, 12·0, 12·0, 12·0, 12·5, 12·0, 12·0. Average=12·12 mm.

Diameter in mm. as measured by most pappus hairs=12·0, 11·5, 11·5, 11·5, 11·5, 12·0, 11·5, 11·5. Average=11·62 mm.

As the efficiency of the pappus would seem to depend on the surface formed by the mass of pappus hairs rather than upon the few longer hairs, 11·62 mm. was taken as the average diameter of the pappus surface. The average area of the pappus surface, therefore, is 1·06 sq. cm.

Angle of the Axis. As the fruit was in movement during dispersal observations were not accurate. The angle of the axis with the horizontal appeared to vary between 45° and 60°. Photographic measurement should be possible and will be used in subsequent experiments.

Rate of Fall in Quiet Air. The determination of this constant by Praeger (30) is taken as sufficiently accurate and is converted into m.p.h.; 12 feet in 8·5 seconds=·98 m.p.h.[1]

The Vertical Component. In the experiments described in Section B the wind was always lateral, so that a wind with the minimum or critical vertical component also had a horizontal component. Any wind-pressure which lifted the fruit when it had once fallen was, therefore, due to a wind, the total force of which exceeded the critical vertical component. This component is taken to be the pressure of the maximum wind which does not blow the fruit more than 4 cm. (see below under Winds between " W " and " V "). The chief source of error in the experiment is the friction

[1] This is calculated from the rate of fall (12 feet in 8·5 seconds) recorded by Praeger. He gives inversion of the time and multiplication by 8 as a method for approximating in m.p.h. the observed rates of fall in secs. per 12 feet. A closer approximation is obtained by using 8·4 instead of 8 and this has been used in the present calculations.

between the glass and the fruit, but in the case of the dandelion the fruit rests on the glass on the tips on a few pappus hairs and a very small portion of the surface of the fruit body. Friction in such a case is reduced to a minimum. Another possible source of error is the adhesion of the fruit to the glass; this might arise from a mucilaginous pericarp or from mucilaginous achenial hairs, both of which are absent in the dandelion, so that this source of error is eliminated. A third possible source of error is the assumption that the effect of the tangential component S is negligible but this assumption is justified by subsequent observation and calculations.

With the dandelion the observed maximum wind which does not move the fruit is 1·01 m.p.h. (see table X) and in this case it can be taken as the velocity of wind with a pressure equal to the critical vertical component, ·0026 gms. per sq. cm.

Theoretical Conclusions.

From these observed data various conclusions can be drawn, and the more interesting points will now be considered.

Fall in Quiet Air. The first interesting point arises from the close similarity between the rate of fall in quiet air, ·98 m.p.h. and the experimental value found for the critical vertical component, which is equivalent to 1·01 m.p.h. This is easily explained from the hydrodynamical point of view. In still air there is no lateral force, therefore there is no tilting of the fruit. The pappus surface is horizontal, so that there are two forces acting during the fall, the mass of the fruit and the pressure exerted by the air impinging on the pappus with a velocity equal to the rate of fall. The latter force is similar to that acting with a lateral wind but in this case it all acts in a vertical upward direction. The mass of the fruit acts downwards in a vertical direction.

The fruit in quiet air rapidly acquires the terminal velocity of fall, then the upward force is equal to the downward force, the fall being due to the momentum gained before the terminal velocity is reached. The upward force due to a fall at the rate of ·98 m.p.h. is equivalent to a wind with a velocity of ·98 m.p.h. The experimental value, 1·01 m.p.h., found is quite a close approximation, especially when it is remembered that, as Praeger mentions, there is some variation in fruits collected from different heads, although those from the same head are very similar. The rate of fall in quiet air is at least approximately equal to the velocity of the critical vertical component and is more easily and accurately measured by

the method of Dingler and Praeger than by the rather tedious method adopted in the present investigation.

The Critical Vertical Component. Although the pressure and the velocity equivalent to the pressure of the critical vertical component can be calculatd as shown in Section B from the known pressure of the maximum wind which does not move the fruit, the actual value of the pressure on the pappus can be determined only when the area of the pappus is known. This constant as shown above is 1·06 sq. cms., therefore the pressure of the critical vertical component on the area of the pappus is ·0026 x 1·06=·002756 gms.

The Efficiency of the Pappus. If the pappus acted as a continuous membrane the total pressure of the critical vertical component would be equal to the weight of the fruit, but the hairs of the pappus do not form a continuous membrane. Some of the wind passes between the hairs and exerts no effective pressure. The pressure actually exerted on the pappus by the critical vertical component, is, of course, equal to the weight of the fruit, so that the fraction $\dfrac{\text{pressure actually exerted on the pappus}}{\text{pressure of V on the area of the pappus}}$ gives the efficiency of the pappus as a sail or wind-holding mechanism. This efficiency is, therefore, $\dfrac{·000756}{·002756}=·27$.

The Minimum Wind for Dispersal. In discussing the resolution of the pressure in Fig. 27 the fruit was regarded as stationary, but it is in motion during dispersal. The point of view upheld by previous investigators is that the fruit rapidly attains the velocity of the wind which is dispersing it. A little consideration of the diagrams in Fig. 27 will make it quite clear that H, the horizontal component, is considerably less than M, the total pressure, when the fruit is at an angle of 45°. If the fruit were vertical, H would be eliminated and the mechanism would act only as a balloon. On the other hand if the fruit were almost horizontal (*i.e.* the pappus almost vertical) V would be small compared with H. Even in the latter extreme case, however, although H would be almost equal to M, the efficiency of the pappus being only ·27, the horizontal component H would have only the effect of M x ·27. It is clear then that, even when H attains its maximum value, the velocity at which the fruit would be blown would be less than the velocity of M and therefore the fruit would never attain the velocity of the wind.

From the preceding data it is possible to calculate the minimum wind required for dispersal of the fruit to a distance which

is limited only by the presence of obstacles such as trees and mountains, and by the relative humidity of the atmosphere.

FIG. 28.   For explanation see text.

Considering Fig. 28, let

W=pressure of the minimum wind for dispersal,

w=velocity equivalent to W,

M=pressure of the effective part of W,

m=velocity equivalent to M, *i.e.*, the rate at which the wind overtakes the fruit moving with the velocity of h.'

R=normal component of M,

S=tangential component of M (*i.e.*, surface slip),

H=horizontal component of R,

H'=pressure exerted on the pappus by H,

h'=velocity equivalent to H',

V=vertical component of R,

θ=angle of axis of fruit with horizontal.

Since the value of V is M $\cos\theta$ $\sin\theta$, the minimum wind required for dispersal will depend on the value of $\cos\theta$ x $\sin\theta$ and thus on the angle at which the fruit is tilted.   The product of $\cos\theta$ x $\sin\theta$ varies from + ·5 to —·5 and reaches its maximum value of +·5 when θ=45°.   The position of the fruit in which M $\cos\theta$ $\sin\theta$ reaches its maximum value for any given wind is, therefore, with the axis of the fruit at 45° to the horizontal.   Since any wind which is able to lift the fruit will carry it along, the minimum wind which will disperse the fruit will be the one with which the fruit assumes an angle of 45°.   The value of θ in this particular case is, therefore, 45°.   An angle of 45° for the pappus (with the fruit in the normal position) is the usual one for the pappus in the

Compositæ, another example of the efficiency in detail which is characteristic of the family.

$$\text{With } \theta=45°, \text{ V}=\text{M} \cos\theta \sin\theta=\cdot 5 \text{ M}$$
$$\text{H}=\text{M} (\cos\theta)^2=\cdot 5 \text{ M}$$
$$\therefore \text{ H}=\text{V and M}=2 \text{ V}$$

the value of V as determined experimentally is ·0026 gms. per sq. cm.

∴ H=·0026 gms. per sq. cm. and M=·0052 gms. per sq. cm.

The efficiency of the pappus as calculated from the known value of V for the area of the pappus and from the weight of the fruit is ·27.

∴ H′=·0026 x ·27=·0007 gms. per sq. cm.

The pressure M depends on the velocity with which the wind overtakes the fruit as it moves along and the velocity of the effective part of the wind is the difference between the velocity of the wind and the velocity of the fruit, *i.e.* m=w—h′ (∴ w=m + h′).

The pressure M (·0052 gms. per sq. cm.) is equivalent to a velocity of 1·44 m.p.h., *i.e.*, m=1·44 m.p.h.; the pressure H′ (·0007 gms. per sq. cm.) is equivalent to a velocity of ·53 m.p.h., *i.e.*, h′=·53 m.p.h., but w=m+h, ∴w=1·44+·53=1·97 m.p.h.

In this way we find that the minimum wind for dispersal has a velocity of 1·97 m.p.h.,which is equivalent to a pressure of ·0097 gms per sq. cm. Referring to Table X we find the critical pressure A is .0107 gms. per sq. cm., which is equivalent to 2·06 m.p.h. At the next point taken in the experiment the velocity had fallen to 1·84 m.p.h. : the fruit skimmed along the tube, touching it with the base only, being thus partially supported and leaving the wind free to exert a pressure sufficient to blow the fruit right out of the tube. The critical pressure A in the case of *Taraxacum officinale* is clearly an approximation to the pressure of the minimum wind required for dispersal. Whether it is so for other species remains to be determined.

In the case of the dandelion we thus arrive at the interesting conclusion that the critical pressure A is approximately equal to W, the pressure exerted by the minimum wind necessary for dispersal, and that the critical pressure B is approximately equal to V, the pressure of the minimum vertical wind which will support the fruit *i.e.*, the pressure of the minimum or critical vertical component of the effective part M of the horizontal wind W. In the language of aeronautics 1·44 m.p.h. is the minimum speed of the dandelion fruit ; the difference in the two cases is that so long as the aeroplane

overtakes the wind at not less than 60 m.p.h. it stays up, and so long as the wind overtakes the fruit at not less than 1·44 m.p.h. the fruit stays up.

Winds between "W" and "V."—If the wind exerts a pressure of ·0107 gms. per sq. cm. the fruit is blown right through the tube without touching, and if the wind exerts a pressure of ·0026 gms. per. sq., cm. or less, the fruit does not move once it has fallen. Between these two points the fruit moves but touches the tube, and it is of interest to follow the action of the wind with pressures between W and V.

In the initial stages of flight the wind exerts its full pressure, *i.e.*, M=W, but as soon as it has developed an effective action the fruit moves and M becomes less than W. Since the continued flight depends on V being not less than the critical value the fruit will fall : thus if W=·0052 gms. per. sq. cm. M will be less than that and V will be less than ·0026 per sq. cm., which is the minimum vertical component which keeps the fruit up ; the fruit will therefore fall. When reference is made to Table X it will be noted that if W is greater than ·0052 gms. per sq. cm. the fruit moves along continuously but is partly supported by the tube. It is only when W falls below the minimum value of M that the fruit actually stops.

If W is less than ·0052 gms. per sq. cm, then V can never, even in the initial stage, be as much as ·0026 gms. per sq. cm., so that the fruit must fall ; but the time taken to fall will depend on the upward pressure exerted by the vertical component. The fruit will fall slowly if V is nearly ·0026 gms. per sq. cm., and more quickly the smaller the value of V becomes.

The value of V depends on the value of W and on the value of θ. The product $\cos\theta \times \sin\theta$ diminishes gradually until when the fruit is vertical it is nothing. The smaller W becomes the greater θ becomes, because the pappus is not blown so much before the fruit body, so that the smaller W becomes the smaller becomes $\cos\theta \times \sin\theta$, and therefore V becomes smaller very rapidly.

As soon as W is equal to the rate of fall in quiet air the axis of the fruit becomes vertical ; then there is no vertical component of W and the fruit falls with a velocity equal to that of the wind. The initial elevation is then equal to the distance travelled by the fruit. This may be made clear by considering the parallelogram of forces in Fig. 27, D. The force X is equal to the force Y, and they act at right angles to each other, the resultant is AC, which is the path of fall of the fruit. It is then clear that AB=BC,

i.e., the distance travelled by the fruit is equal to the initial elevation. The force X is different from the pressure M or W in that the fruit is being carried along as a balloon is carried along with a velocity equal to the velocity of the wind.

From the above it is clear that what is really measured in the experiments on the critical pressure B described in Section B is not the minimum vertical component of M but the rate of fall, which is, however, equal to the latter constant. It would be possible to measure the critical vertical component directly with a modified apparatus, and the writer hopes to continue the investigation.

The conclusion to be drawn from the experimental and theoretical treatment of the hydrodynamics of the dispersal of the dandelion fruit may be stated briefly thus—so long as the relative humidity of the air remains above ·77 and so long as the fruit does not encounter an obstacle, a horizontal wind of 1·97 m.p.h. is sufficient for its dispersal to any distance.

If the air becomes moist the pappus closes up and the fruit falls rapidly. The problem of surmounting low obstacles is partly solved by the elongation of the scape, which takes place during the twenty-four hours before the fruits are ready for dispersal. The scape elongates 50% to 90% of its original length, *e.g.*, from 24 cms. to 38 cms. and from 20 cms. to 38 cms. in cases which were measured. This sudden elongation is due to a stretching of only the upper part of the scape: the stretching causes the elongated part to be paler incolour since the chlorophyll is not increased in proportion to the increase in surface. The physiology of the phenomenon seems to be somewhat as follows—during the ripening of the fruits there is a marked streaming of carbohydrates up the scape to the capitulum. This streaming does not cease immediately on the maturation of the fruits, and the materials accumulate in the upper part of the scape. This causes the osmotic pressure and the turgidity of the cells in that region to increase so much that the cell walls are stretched along the line of least resistance, *i.e.*, longitudinally. Accurate experiments are, however, necessary to prove this conclusively, and the point appears to be of general interest in view of the similar quick elongation of the supporting stalk in the spore-dispersal of many Bryophyta, and the similar but slow elongation in the peduncles during the fruiting stage of many Angiosperms. Beeby (3) observed similar elongation in the scape of *T. spectabile*, var *maculiferum*, but was " not able to give exact details concerning the times at which

elongation takes place." Cassini (8) had previously recorded the phenomenon in *Tussilago Farfara* and *Chevreulia stolonifera* but gave no details.

The Hydrodynamics of Fruit-Dispersal in other Species.

The theory of the experiments with the other fruits is complicated by the angle at which the pappus spreads in *Senecio, Ursinia* and *Centaurea,* by the presence of mucilaginous achenial hairs in *Senecio,* the presence of a basal tuft of hairs in *Ursinia* and the absence of a pappus in *Leontopodium.* The structure is in no case that of a simple parachute with the wind-holding surface at right angles to the axis of the fruit, as in *Taraxacum.*

Senecio vulgaris, L.—According to Praeger the fruit of *Senecio vulgaris* falls in quiet air at the rate of 12 feet in 12·8 seconds, which is approximately ·66 m.p.h. This is considerably lower than the value (1·18 m.p.h.) obtained for the velocity equivalent to the critical pressure B in this species. There are several sources of inaccuracy, but if ·66 m.p.h. is taken as the velocity of the critical vertical component, it is possible to make a rough calculation of the minimum wind for dispersal. The efficiency of the pappus can be taken as approximately ·25 and calculating as in the case of *Taraxacum,*[1] the minimum wind for dispersal is 1·25 m.p.h. This is quite a good approximation to the value (1.48 m.p.h.) found for the velocity equivalent to the critical pressure A in the experiments described above.

Centaurea imperialis, Hausskn.—As Praeger does not give the rate of fall in this species an approximate measurement of this constant was made by his method and the value found was 2·2 seconds for a fall of 12 feet. This is equivalent to 3·81 m.p.h. Calculating as before we get 7·3 m.p.h. as the minimum wind for dispersal. These two values (7·3 and 3·81) are sufficiently near the experimental values (7·2 and 3·0) found for the velocites equivalent to the critical pressures A and B to show that the methods of experiment and calculation are both approximations to the actual values of the two constants.

Ursinia speciosa, DC.—The rate of fall was determined in this case also for the purpose of this calculation. The value found was 3·4 seconds for a fall of 12 feet. This is equivalent to 2·47 m.p.h. Calculating as before we get 4·7 m.p.h. as the minimum wind for dispersal. These two values (4·7 and 2·47) are quite good

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[1] The tilting of the fruit need not occur in this case as the pappus is already at an angle with the horizontal.

approximations to the experimental values (4·5 and 2·1) obtained for the velocities equivalent to the critical pressures A and B· The minimum wind for dispersal in these three species is clearly approximately the same as the minimum wind required to blow the fruits out of the tube without a pause. It is also closely approximate to the value calculated from the rate of fall assuming the angle to be 45° and the efficiency of the pappus to be ·25. We have, therefore, a convenient although somewhat rough method for the calculation of the minimum wind required for the dispersal of those pappose fruits of which the rate of fall in quiet air is known.

Leontopodium alpinum, Cass.—These fruits not being pappose the preceding methods do not apply, and as they are spherical the dispersal is more analogous to spore dispersal or to the cases given by Thoulet (35) and Udden (37), see section D. Considering the very slow winds which are sufficient for the dispersal of spores it is probable that the velocity (4.4 m.p.h.) equivalent to the critical pressure A is at least an approximation to the minimum wind for dispersal in this species. It is interesting to note that, although Stokes' Law may apply in this case, the cypsela in the Compositae when epappose is usually cylindrical. It has been shown by Eiffel (13) that a cylinder has a much slower rate of fall than a sphere of the same diameter, for instance, if the length of a cylinder is equal to the diameter and the movement is in the direction of the axis, the resistance of the air is five times greater than it is for a sphere of the same diameter moving at the same rate.

D. Phylogenetic Significance of Fruit-Dispersal.

The significance of the hydrodynamics of fruit dispersal may not be immediately obvious, but the question of whether a given fruit requires for its dispersal a wind of 2 m.p.h. or a wind 50 m.p.h. is of fundamental importance in the interpretation of the facts of geographical distribution. A proper understanding of the conditions of wind-dispersal is necessary for the rational study of the history of the Compositae, their migrations and colonisations, their paths of travel and regions of concentration, which form the subject of the following chapter.

De Candolle (11), who is followed by Bentham (I, 7), Praeger (30), Willis (IV, 94) and others, ignores or gives rather unsubstantial reasons for neglecting the authentic evidence for wide dispersal, and gives a series of negative observations in support of the dispersal for short distances only. That such generalisations from particular

observations are not sound is amply proved by the cases recorded by Treub (36), Penzig (29), Ernst (15), Gates (19), Vogler (38-40) and others (see Sect. A), and the argument given by Wallace makes it clear that negative evidence in this matter has very little value. Further evidence of the transporting power of wind is given by Udden (37), who showed that particles between ·001 mm. and ·04mm. are apparently completely borne up by a wind of 8 m.p.h. Thoulet (35) states that a hailstone 5 mm. in diameter could be sustained in the air by a wind of about 22 m.p.h. and one of 10 mm. diameter by a wind of about 33 m.p.h. After summing up the available evidence on the dispersal of dust particles Evans (16) says, "In any case, it is sufficiently demonstrated that particles of detritus up to about 100 microns in diameter, . . . , are capable of remaining suspended in moving air for an indefinite period. A very moderate wind will carry them along with it, and a slight unevenness of the surface is sufficient to give rise to an upward current of the air, which will raise its freight of minute mineral particles high above the ground."

Since dust particles of the size mentioned have a rate of fall which is two to four times that of the average pappose fruit, it is not unreasonable to suppose that moving air will have an effect on such fruits equal to its supporting effect on more or less spherical particles which are not so well adapted for dispersal by wind.

It has been calculated by Udden (see Evans, 16 p. 254) that in the west of the United States an average of about 850,000,000 tons of dust is carried 1,440 miles in each year. It is not unreasonable to suppose that such a weight might include some pappose fruits, which have an average buoyancy more than equal to the buoyancy of the larger particles of dust. Evans also refers to observations of particles of sand as much as ·2 mm. in diameter being blown from the Sahara as far north as Hamburg. As the rate of fall of such particles is considerably greater than that of most pappose fruit this is further evidence for the probable dispersal of such fruits to considerable distances. Spherical fruits such as those of *Leontopodium alpinum* with a diameter of ·25mm would be transported long distances at least as easily as grains of sand ·2 mm. in diameter.

Praeger (30, p.72) also mentions that "thistle down was watched half a mile from the shore blowing seaward, and in every case its course was practically a straight line." It is quite clear that the theoretical view adopted by Praeger, that particles in moving air acquire the same velocity as the air, agrees neither with the

experimental results here given, nor with the theoretical view which enables us to calculate the minimum wind for dispersal, nor with Praeger's observation of the path of the thistle down, nor with Udden's observations on the path of solid particles in an 8 m.p.h. wind. The close accordance of the experimental velocities with the velocities as calculated from the observed rate of fall shows that the relation of the rate of fall to the velocity of the wind required for suspension of the fruit for an indefinite period is at least approximately that discussed in Section C.

The relative humidity of the air, however, has a very marked effect on the efficiency of the pappus as a dispersal mechanism, and the study of the meteorological conditions obtaining in the region of dispersal becomes necessary. In Britain, France, and Ceylon, which are the dispersal regions considered by the above mentioned opponents of long distance dispersals, wind is associated with a high relative humidity and a low relative humidity is associated with calm. The conditions necessary for long distance dispersal are a low relative humidity combined with a wind always above the minimun value of W for the particular fruit and blowing in the same direction over a large stretch of land or water. These conditions are comparatively rare in northern Europe and in Ceylon, but occur occasionally in most of the regions in which long distance dispersal has been observed.

As a result of the above investigation the writer has reached the conclusion that given these three conditions there is no limit to the distance of the dispersal of pappose fruits, and with this conclusion Dr. J. W. Evans, from his experience of the dispersal of sand, is in complete agreement. The occurrence of pappose species with a limited distribution is quite in accordance with the Law of Age and Area which will be discussed in the next chapter. The comparison by Bentham (I, 7) of the local species of *Senecio* with wide spread species of epappose genera is an example of the special pleading which has been used to explain away the obvious fact that the pappus-mechanism is an efficient means of dispersal. De Candolle's comparison by percentages of pappose and epappose species in the various tribes (11) is just as superficial. Before such comparisons (or one of wide spread pappose species with local epappose species) can be used every factor in the two cases must be balanced. These factors would include age, other means of dispersal, available habitats, the environment in which the journey starts and ends, colonising powers, physiological

differentiation, morphological differentiation during the life of the species, etc. Such a comparison has not yet been made.

The results of the present investigation which will be valuable in the subsequent study of the geographical distribution of the Compositae are (1) that the ordinary pappose fruit under the proper meteorological conditions can be blown many hundreds of miles over land or sea, (2) that hypothetical land bridges are not necessary to explain the present distribution of the Compositae, so that we can take the world as it is without raising and sinking continents, as Darwin (10) says " in a quite reckless manner." This latter is an important point as the Compositae are almost certainly of such recent origin that the possibility of land bridges is in many cases quite out of the question.

In order to facilitate reference the following summary is given of the minimum velocities of wind necessary for the dispersal of the species investigated, together with the expressions for winds of such velocities (cp. 46. p. 161)

TABLE XI.

Species.	Experimental Value in m.p.h.	Calculated Value in m.p.h.	Common Name of Wind.
Taraxacum officinale, Weber ...	2·06	1·97	Light Breeze.
Seneeio vulgaris, L.	1·48	1·25	Light Air.
Senecio vulgaris, L. ... ... var. *radiatus erectus,* Trow	1·76	—	Light Breeze.
Tussilago Farfara, L.	·59	—	Less than a Light Air.
Centaurea imperialis, Hausskn ...	7·2	7·3	Moderate Breeze.
Ursinia speciosa, D.C.	4·5	4·7	Gentle Breeze.
Leontopodium alpinum, Cass ...	4·4	—	Gentle Breeze.

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FIG. 1. *Rhodymenia palmata.* ½ nat. size. a. primary portion. b. secondary fronds. c. tertiary growths.

FIG 2. *Callymenia Lateriæ* Holmes. ½ nat. size. a. frond. b. new growths.

LYLE—DEVELOPMENTAL FORMS OF MARINE ALGÆ.

FIG. 1. *Nitophyllum litteratum.* ½ nat. size. a. old fronds. b. new leaflets.

FIG. 2. *Nitophyllum litteratum.* ½ nat. size. a. primary portions. b. secondary portions. c. tertiary growths.

FIG. 3. *Callymenia reniformiis.* ½ nat. size. a frond. b. new growths.

LYLE—DEVELOPMENTAL FORMS OF MARINE ALGÆ.

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DEVELOPMENTAL FORMS OF MARINE ALGAE.

BY LILIAN LYLE.

(WITH PLATES I. AND II. AND TEN FIGURES IN THE TEXT.)

OF the various points of view from which Marine Algæ may be regarded, their plasticity of form, and response to changes in surrounding conditions afford peculiar interest and have attracted considerable attention.

The dimorphism of *Nitophyllum ramosum* Batt. (*Nit. laceratum* Grev.) is a case in point. At times the normally erect thallus takes on a procumbent position. The resemblance to *Nitophyllum reptans* is then so close as to lead one to suspect that the two species may be identical.

The species *Nitophyllum reptans* has been described by Crouan[1] and Zanardini[2], but as shown in the following notes, the plant is really a prostrate stage of *N. ramosum*, and is accordingly removed to that species.

The note on Recrudescence is tentative, referring to certain growth forms and their possible origin, such as changes in tissue substance, mechanical irritation, etc.

I have to express my sincere thanks to Miss Lorrain Smith and Mr. Gepp, both of the British Museum (Nat. Hist.), for their valued suggestions.

NITOPHYLLUM RAMOSUM (*Nit. laceratum* Grev.) f. *reptans*. comb. nov. (*Nitophyllum reptans* Crn.), Figs. 1-13.

After carefully examining a series of specimens of *Nitophyllum reptans* Crn. and *Nitophyllum ramosum* Batt. I have come to the conclusion that they belong to the same species, and that *N. reptans* is an occasional, prostrate and dorsiventral form of *N.*

[1] Crouan. Flore de Finisterre, p. 153.

　　　,,　　1851. Ann. Sci. Nat., T. xv, Sér. III, Gen. 146, p. 365.

[2] Zanardini. Icon. Phyc. Adriat., Vol. III, p. 85.

ramosum. The dorsiventralism in this case, being due to certain conditions of growth, arises only in the initial stages of the plant, but may persist throughout its life cycle.

The procumbent form of *N. ramosum* Batt. grows on the stipes of *Laminaria Cloustoni* and on *Lithothamnion polymorphum*, where it adheres to the rough surfaces, afterwards sending up
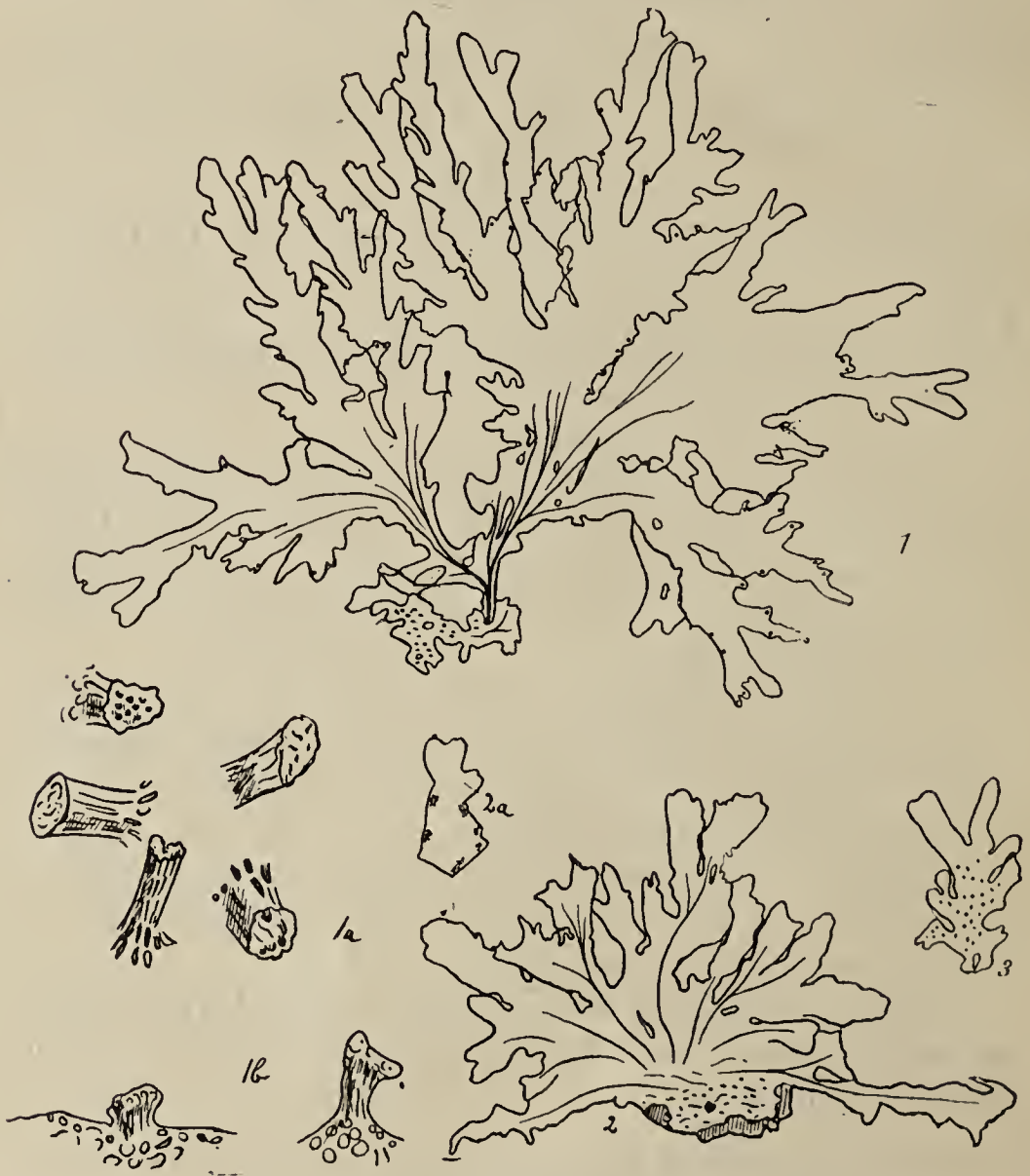
FIGS. 1, 2. Thallus of *Nitophyllum ramosum* showing procumbent portion at base, with sucker-like appendages. FIG; 1a. Sucker-like appendages of *N. ramosum.* x 20. FIG. 1b. Ditto of *N. ramosum.* f. *reptans.* x 20. FIG. 2a. Tetrasporanges of *N. ramosum.* FIG. 3. Thallus of *N. ramosum* f. *reptans.* All figures half nat. size.

erect shoots, Figs. 1, 2. The under surfaces of the dorsiventral portions are provided with the sucker-like rhizoidal processes, the suckers characteristic of *N. reptans,* Fig. 3, and, if detached, would be taken for fragments of the latter, Figs. 1a, 1b. A

DEVELOPMENTAL FORMS OF MARINE ALGÆ.

By Lilian Lyle. (Vol. XVII, No. 10.)

Corrigenda.

The magnification of the text figures on pp. 232, 233, and 234 should all be *doubled*. For ×20, *read* ×40, *for* half nat. size *read* nat. size, and so throughout. The magnifications of the figures on Plates I and II are correct.

specimen of *N. reptans* in the Herbarium of the British Museum, found on a stem of *Laminaria Cloustoni*, corresponds in appearance to some procumbent portions of *N. ramosum* gathered from a similar habitat.

As regards structure *N. reptans* is monostromatic and veined. *N. ramosum* is also monostromatic in its upper, younger, and also in the procumbent portions. The cells of *N. reptans* measure 30 x 40μ, those of *N. ramosum* are 35 x 50μ, but any difference in size may be accounted for by the difference in plane, age and habit. The shape is of much the same roundish oval type, Figs. 4, 5.
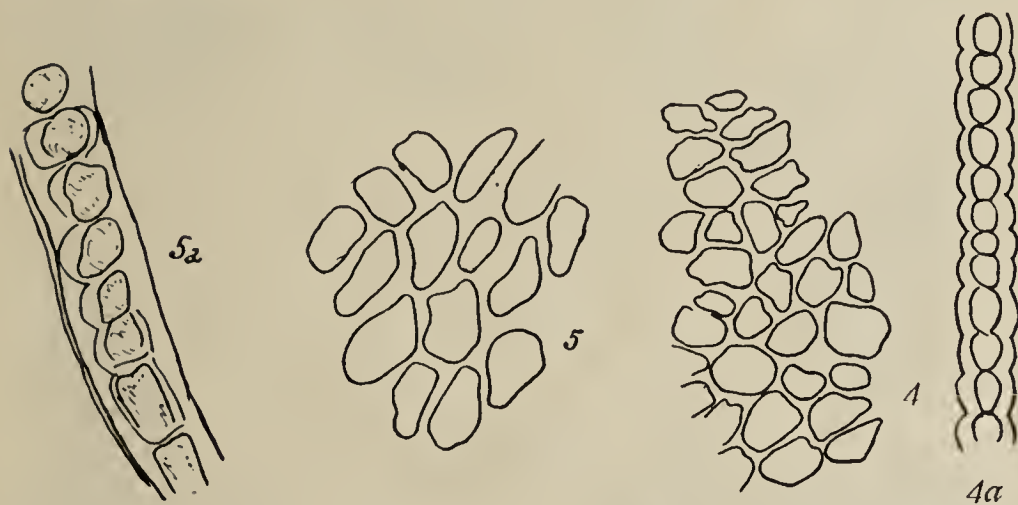
FIG. 4. Cells from thallus of *N. ramosum* f. *reptans*. x 62. FIG. 4a. Transverse section of thallus *N. ramosum* f. *reptans* from Crouan's *Flore de Finisterre*, Pl. 21, f. 140 bis. FIG. 5. Cells from thallus of *N. ramosum*. x 62. FIG. 5a. Tranverse section of thallus of *N. ramosum*. x 62.

The thallus of *N. reptans* is formed in rounded lobes, that of *N. ramosum*, though branched, also ultimately bears, rounded lobes.

Crouan has described the cystocarps of *N. reptans* as spherical, placed towards the tips of the lobes[1], Fig. 6. The position of the cystocarps in *N. ramosum* v. *Smithii* Batt. is similar[2]. In both cases, as has been described for *N. reptans*, they are " sessile on the frond, hemispherical, composed of moniliform sporiferous filaments on a prominent basal placenta, and enclosed in a pericarp of very thin cells "[3], Figs. 7, 8.

The tetraspores of *N. ramosum* are borne along the upper margins of the frond, either in round or elongated patches, with a tendency to

[1] Crouan. 1851, *loc. cit.* Flore de Finisterre, p. 153.

[2] ,, Flore de Finisterre, 152.

[3] Zanardini, *loc. cit.*

become confluent, or they occur in special proliferations. Hitherto the tetraspores of *N. reptans* have not been discovered. It was my good fortune to find a plant with a well marked line of marginal tetraspores exhibiting the same characteristics as those of *N. ramosum*, Figs. 9, 9a.

Fig. 6. Cystocarp of *N. ramosum* f. *reptans*, from Crouan's *Flore de Finisterre*, Pl 21, f. 140 bis. Fig. 7. Trans. sect. of *N. ramosum* f. *reptans*, from Crouan's *Flore de Finisterre*, Pl. 21, f. 140 bis. Fig. 8. Trans. sect. *N. ramosum.* x 31½.

Fig. 9. Tetraspores of *N. ramosum* f. *reptans.* Half nat. size. Fig. 9a. Tetraspores of *N. ramosum* f. *reptans.* x 20.

Fig. 10. Frond of *N. uncinatum* adhering to other algæ (shaded portions). Half nat. size. Fig. 11. Sucker-like appendages of *N. uncinatum.* x 20. Fig. 12. Cells from frond of *N. uncinatum.* x 62. Fig. 13. Procumbent portion of *Gelidium crinale.* x 20.

The procumbence of *N. reptans* is probably of advantage to it under conditions which would be inimical to an erect position, *e.g.*, where exposed to great force of waves, moving stones, etc. This plant is moreover distinctly an inhabitant of deep water.

N. reptans therefore merely ranks as a form to be expressed thus, *Nitophyllum ramosum* f. *reptans.* It may possibly even come to be considered only a growth phase.

A. D. Cotton in his Clare Island Survey suggested a possible connection between *N. reptans* Crn. and *N. uncinatum* J. Ag.

Fig. 10.[1] It is true that the latter does sometimes assume a procumbent form when attaching itself to other algæ, and also puts forth little sucker-like rootlets from the hooked portions of the thallus, along the exterior margins and occasionally from the flat surfaces, Fig. 11; but here, I think, the connection ends. The structure of *N. uncinatum* is polystromatic, with oblong, cylindrical to hexagonal cells, Fig. 12. The sori are round and solitary, on short trifoliate obtuse lobes : they rarely occur on the frond itself.

The whole genus *Nitophyllum* is very variable, and possibly of so plastic a nature that it responds readily to any stimulus; that of contact excites further growth, resulting in the development of suckers or rhizoid projections as need arises.

In corroboration of these points Harvey has noted " the marked difference between the same species found at different depths," and again " the tendency of specimens from deep water to form both hooks and discs, or supplementary roots, from various points of the stem and branches." He also remarked that " the outward habit is so completely changed by the production of hooked processes and discs, that it is difficult to discover the affinity of these distorted forms and such specimens have occasionally been unduly elevated to the rank of species."[2]

Occasional dorsiventralism is not confined to this genus. It occurs in *Gelidium crinale*, a plant usually erect in habit, but it has been found at low tide creeping over *Lithothamnion polymorphum*, when it sends down little root-like suckers from its under surface. Intermediate stages exist in sandy conditions where the plant is partially erect, partially creeping. The interlacing fibres serve to hold the sand together and form tufts or knots of vegetation, Fig. 13. Yendo[3] refers to *Gloiopeltis* and other algæ, which are membranaceous in the embryonal stage adhering firmly to the substratum. Doubtless other instances will be forthcoming as a result of further research.

RECRUDESCENCE. Pl. I, Figs. 1-2 and Pl. II, Figs. 1-3.

Certain lateral and superficial growths have been noticed on the older plants of several species, and questions as to their biological significance naturally arise.

[1] Cotton, 1911. Clare Island Survey, p. 136.

[2] W. H. Harvey, Substance of a course of Lectures on Marine Algæ, 1856. Opuscula Crypt. LXXIII, p. 87.

[3] Yendo. Economic Proc. Roy. Dublin Soc., V, II, No. 7. March, 1914, p. 118. See footnote.

They begin as proliferations, and extend indefinitely, eventually equalling or exceeding in size the parent plant. In some cases they may even bear secondary growths or proliferations which repeat the characteristics of the primary ones.

Rhodymenia palmata, Nitophyllum Hilliæ, Nit. litteratum, Callymenia reniformis, Call. Lateriæ and Callophyllis flabellata all exhibit these growths.

In the case of the first named, Pl. II, Fig. 1 a, b, c, the original plant persists as a small disk, a short stalk, and the base or remnant of lamina, all else having disappeared, either by wave action or by some other cause, Fig. 1a. It is horny, dull brown, about 3 cms. wide and 1½ cm. high. From this proceed almost sessile or shortly stalked wedge-shaped, ribbon-shaped, or irregular fronds measuring 15-43 cs. in length and 2-4½ cs. in width. The ends are much broken. Their substance is coriaceous, deep brownish red with wrinkled, and finely pitted surfaces, owing perhaps to the formation and escape of tetraspores, Fig. 1b. Upon these fronds are born, yet further shortly stalked laminæ, some of which are ovate and entire, others cuneate or strap-shaped, bifid and emarginate. These latter developments are thin, becoming pale and transparent towards the extremities, the bases dark red, Fig. 1c. In the Batters collection at the Natural History Museum there is a striking example of this form of growth which, it is worthy of note, is not placed among the specimens of var. *marginifera*.

Another plant of *Rhodymenia palmata* shows the surface covered with proliferations curiously thick in texture and of a pale red. They are easily detached and give the impression of being young plants. The frond is old and is shaded from yellowish red to dull yellow. The new growths on the margins are much larger than those on the surface and are deeply indented.

It is known that tetraspores can germinate and grow while still embedded in the parent plant, but the proliferations described above can hardly have arisen in such a manner as they are of various sizes and stages of developement.

A curious instance occurs in a specimen of *Nitophyllum litteratum*, which consists of two fronds, old and strongly veined. Both are thickly ringed with new growths, mostly wedge-shaped, some quite small, others larger than the primary plant, Pl. II, Fig, 1 a, b.

Another plant of the same species gathered from an exposed situation is more of an extreme case, somewhat resembling the succession of growths observed in *Rhodymenia palmata*. There is

[1] A. & S. Gepp. *Journ. Bot.* 1906,

first the old plant, much torn and discoloured.   From this proceed in all directions stalked wedge-shaped fronds, of distinctly more recent origin than the first.   Upon their sides and surfaces new processes emerge in various stages of developement; these again may bear yet further proliferations.   Pl. III, Fig. 2 a, b, c.

Another species—*Nit. Hilliæ*—shows similar outgrowths.   A specimen was gathered in quite a different locality, where there was moderate shelter; it is very large and old much torn and eaten. New portions are showing from the margins and occasionally from the surface,

The following examples of recrudescence may also be cited. Final flabellations of an old plant of *Callophyllis flabellata* consisting of new tissue expand from narrow bases into quite appreciable flabellate fronds.

A large and very old *Callymenia Lateriæ* Holmes, Pl. I, Fig. 2a, is thickly beset on surface and margins with reniform proliferations.   They are in all stages of growth, and have much the appearance of being new plants produced upon the old one, Fig. 2b.

The same thing is happening on a plant of *C. reniformis* in lesser degree.   It is distinctly old, much torn or eaten, but new growths are issuing from its margin and surface.   Pl. II. Fig 3, a, b.

These structures are evidently growth forms arising as subsequent developments upon mature plants, and are quite distinct from the ordinary proliferations characteristic of a variety or species in which both frond and leaflet are of the same age.   They are the result of tissue recrudescence, but the agencies which have induced it are still unknown.

Mr. Gepp has suggested that the superimposed fronds may represent 2nd and 3rd year growths, and are actual plants developed in " situ " without having been detached.

In the case of biennial and perennial plants, they would there fore be either renewals of growth for each successive year, or represent a process of propagation by proliferation.

The development of new plants upon the old ones, and possibly at their expense, would assure the preservation of fronds until a certain maturity is achieved and they would thus stand a better chance of establishing an independent existance when they break away from the parent.   The specimens under consideration were

found or dredged from deep water in sheltered, moderately sheltered, and exposed situations.

It is possible that when plants are wounded, numerous offshoots arise at the point of injury. I have often observed that *Fucus* fronds, where cut, produce tufts of proliferations—a phenomenon somewhat akin to the growths described above. This subject requires further careful investigation.

THE CONJUGATION OF *ZYGOGONIUM ERICETORUM* KÜTZ.

By William J. Hodgetts, B.Sc.

[With Two Figures in the Text.]

I.—Introduction.

ALTHOUGH *Zygogonium ericetorum* Kütz. (=*Zygnema erice-torum* Hansg.) is such a common alga, occurring either as the terrestrial form on heaths and damp peaty ground generally, or as the aquatic form in peaty water, yet conjugation must be a very rare occurrence with it. Hassall (5) found "union to have taken place between some of the filaments of *Conferva* (*Zygogonium*) *ericetorum*," but states that such a condition is "very rarely met with." He gave no figure and no details.

West and Starkey (10), in their study of *Z. ericetorum*, made numerous cultures of it under various conditions, their work extending over a long period, but were unable to induce conjuga-tion; and they conclude that it "appears very rarely, if ever, to conjugate." West (8) states that *Z. ericetorum* from this stand-point is "on the whole . . . . the most inert and unresponsive alga at present known." Resting cells ("cysts"), akinetes, and aplanospores, however, are not at all uncommon with this species, and appear to be the chief means by which it tides over unfavour-able periods. Fritsch (4), for instance, has recently described an extreme terrestrial form of *Z. ericetorum* which may be said to be permanently in the akinete condition.

De Bary (3), in his classical work on the Conjugatæ, gave a

short account, illustrated with two figures, of the conjugation (as observed in dried material) of *Zygogonium ericetorum*, under the name of *Zygogonium didymum* Rabenh. He considered the latter as probably only a form of *Zygogonium ericetorum*, which is undoubtedly the case. West (8, 10), for instance, has examined the original specimens of *Zygogonium didymum* Rabenh (=*Z Agardhii* Rabenh.) in the herbarium of the British Museum, and states that they are identical in every respect with *Zygnema* (*Zygogonium*) *ericetorum* (Kütz.) Hansg., a conclusion which, it will be seen, is further strengthened by the observations recorded below.

The process of conjugation described by de Bary for "*Zygog. didymum*" is peculiar and does not quite resemble what has been observed in any other member of the Conjugatæ. He states that the conjugating cells (which are in different filaments) put out protuberances which meet and adhere at the extremeties, but instead of fusion taking place and the two cells put in communication by means of a "conjugation-canal," the greater part of the protoplast of each cell passes to the extremity of the protuberance and is there cut off from the main body of the cell—in which, however, a remnant of protoplasm is left—by a curved partition-wall as a special cell or gametangium (3, Plate VIII, Fig. 19,[1] a, b). The thick wall separating the two gametes becomes gradually absorbed, and the latter fuse to form an elliptic zygospore, which surrounds itself with an independeut wall.

The special cell or gametangium, cut of in the protuberance of each conjugating-cell,[2] is exactly comparable to the special gametangia observed in *Temnogametum* and *Sirogonium*. These genera, however, differ from *Z. ericetorum* in the fact that the sterile cells cut off at the same time as the gametangia, each contains a complete protoplast, with chromatophore and nucleus, and resembles an ordinary vegetative cell, while the corresponding sterile cells of *Z. ericetorum*, with their slight colourless protoplasmic contents, are much better compared with the relics of the *gametangia* of *Mougeotia* or *Pyxispora*—in which genera, likewise, the whole of the protoplast of the conjugating cell is

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[1] Reproduced in various works, such as Oltmanns, Morph. d. Algen, Vol. 1, Fig. 41, 6, on p. 66; also Cooke, British Freshwater Algæ, Vol. 2, Plate 40, Fig. 3, c.

[2] The term "progametangia," applied to these conjugating-cells by Wille (13), seems unnecessary; but it should be noted that the word has been applied—quite incorrectly—by several authors to the actual *gametangia* cut off in the conjugation-tubes.

not used up in the formation of the gamete. The affinity of the alga, however, is further discussed below.

Since the publication of de Bary's work (1858) the conjugation of *Z. ericetorum* appears to have been recorded only once, and then under another name. W. & G. S. West (11) in 1894 described a species of *Zygnema* under the name of *Z. pachydermum*, conjugating specimens of which were obtained "from the surface of mud in a warm stream in the crater of Grande Soufrière in the West Indian island of Dominica." The process of conjugation was described as taking place exactly as in those species of *Zygnema* in which the zygospore is lodged in the conjugation-canal (and which were therefore placed by Kützing, in 1843, in the "genus" *Zygogonium*[1]), and no special gametangia were observed to be cut off prior to fusion of the gametes.

Later, West and Starkey (9, 10) very thoroughly re-examined the original material of *Zygnema pachydermum* and found that " vegetatively this alga is identical with *Z. ericetorum* ; " and thus concluded that " *Z. pachydermum* " was a conjugating specimen of the common species. This, if correct, meant that *Z. erictorum*, under the conditions in which it was found in the W. Indies, conjugates in exactly the same way as such a species of *Zygnema* as *Z. Ralfsii*. Further, they considered that since the process of conjugation described by de Bary had not been confirmed by anyone since 1858, that his account of "*Zygogonium didymum* " may have been based on an abnormality ; and that it could not be used as a basis for the genus *Zygogonium*, as proposed by de Bary.

It appears that these conclusions, although reasonable at the time in view of our meagre knowledge of the conjugation of *Z. ericetorum*, must now be modified. since the present writer has been fortunate in finding the typical terrestrial form of *Z. ericetorum* in conjugation, and, as will be seen below, has been able to confirm de Bary's account (described under " *Zygogonium didymum* ") as far as it went, while a few details have been added. It now seems impossible to doubt that *Zygogonium ericetorum* must be kept in a genus apart from *Zygnema*.

[1] For reasons why Kützing's *Zygogonium* cannot be upheld see (8) and (10). De Bary (3) proposed putting the genus *Zygogonium* on a new basis, namely, that of the peculiar process of conjugation observed in "*Zygogonium didymum*" (=*Z. ericetorum*). If this is accepted, then *Zygogonium* contains only one species (*Z. ericetorum*). The subject is further discussed below.
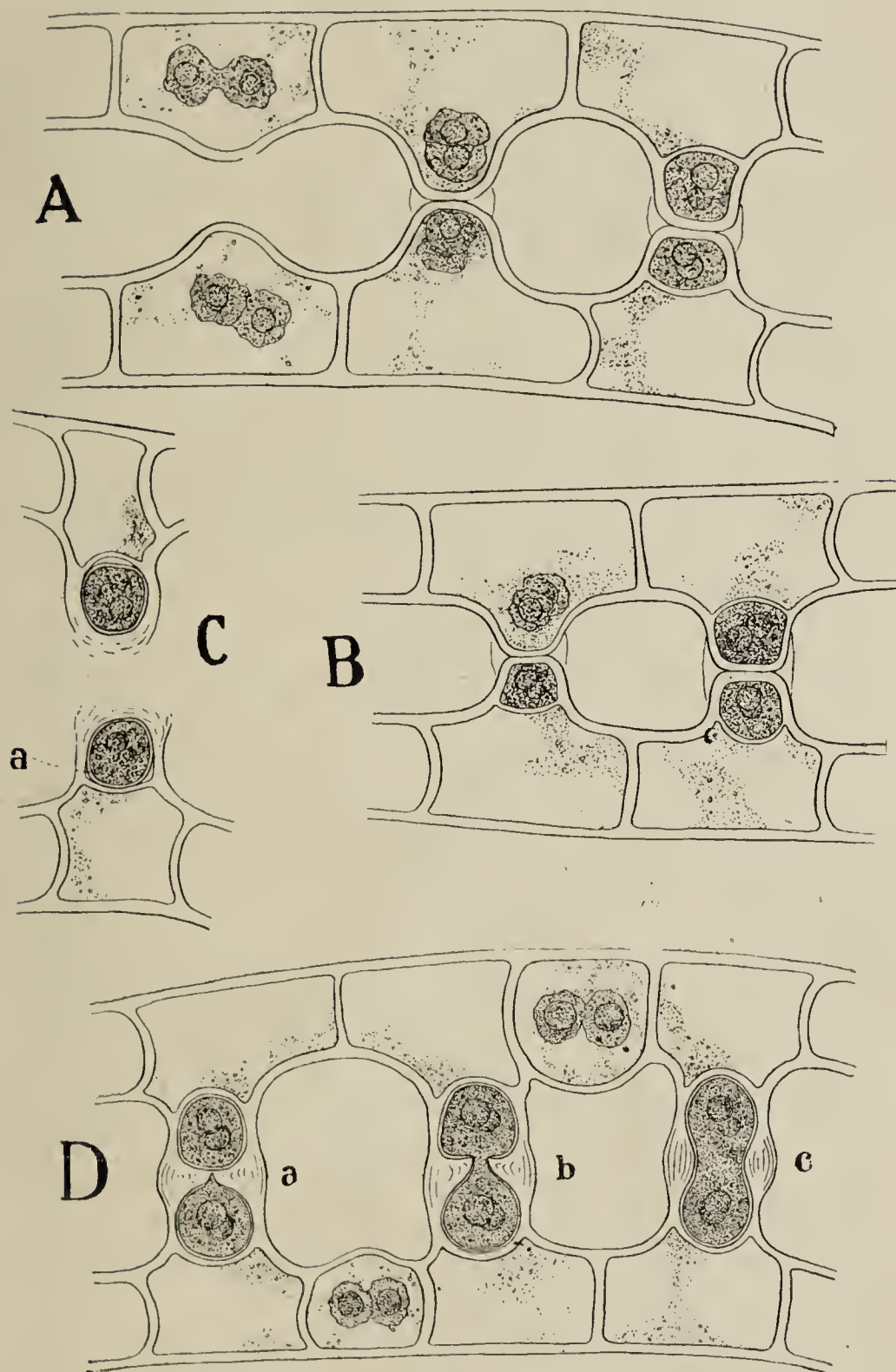
Fig. 1, *Zygogonium ericetorum* : A, early stages in conjugation ; on the right the gametangia are seen to have been cut off. B, ditto, the lower filament being in a more advanced stage of development than the upper one. C, two gametangia, separated in the process of mounting : a = thin inner wall of gametangium ; D, a, very early stage in the fusion of the gametes; b, later stage in ditto ; c, a still later stage.   all × 600

II. Observations on *ZYGOGONIUM ERICETORUM*

The conjugating *Z. ericetorum*[1] occured last July on the surface of damp peaty soil in Wyre Forest, about three miles from Bewdley, Worcestershire, and although the alga was common enough in the vegetative state—mainly as the green-coloured form, phycoporphyrin being generally feebly developed, a result probably of the alga being usually shaded from direct sunlight[2]—yet conjugating filaments were generally rare. Numerous samples were taken, but these proved to be mainly in the vegetative state, showing cytological characters typical of the species, the cell-wall being thick and lamellated, while many of the filaments showed not infrequently short lateral branches; in others conjugating threads were present although somewhat rare. A diligent search, however, resulted in numerous examples being seen, and every stage in the process of conjugation was eventually observed and a number of permanent preparations secured.

Conjugation is always scalariform. Two cells of adjacent filaments put out protuberances which meet, while their extremities become flattened against each other, and adhere, owing to the development of mucilage from the outermost layers of the cell-wall (Fig. 1, A). The actual protuberance is due to the local increased growth of the innermost, more refractive, layer of the thick cell-wall breaking through the less dense outer layers, the wall of the outgrowth becoming thickened as it grows by the deposition of newer internal layers of cellulose. So far the deeply constricted chloroplast in each cell, with its two conspicuous pyrenoids, has undergone no evident alteration, but very soon after the two protuberances meet the chloroplast of each cell becomes much contracted, sometimes even assuming a roughly spherical shape, while the pyrenoids become less conspicuous—although still to be made out by staining with iodine. As the chloroplast contracts it gradually passes into the protuberance, together with the greater part of the cytoplasm, and is there cut off from the body of the cell by a curved partition-wall (Fig. 1, A).

. Each gamete is thus enclosed in a special cell or gametangium, the two being separated by a thick double wall. The main body of the conjugating cell is by no means empty, but contains a notable amount of granular colourless cytoplasm, and

[1] The identification of the alga was kindly confirmed by Prof. G. S. West.

[2] It is probable that the purple pigment in the cell-sap acts as a protective screen against the ill-effects of strong sunlight—see Fritsch (4) and the literature there cited.

sometimes a few small oil globules, but no nucleus.[1] In the fact that the entire protoplast is not used up in the formation of the gamete *Zygogonium ericetorum* differs from *Zygnema,* but resembles *Pyxispora* and also *Mougeotia* (see discussion below).

The curved wall which cuts off the gametangium is rather thin, and gives the usual reaction for cellulose. It is generally very convex, sometimes almost hemispherical, while it projects a variable distance into the lumen of the sterile cell—sometimes half-way across the latter. Very rarely is it almost plane. Although the two apposed gametangia were observed to be cut off generally at about the same time, yet in several instances one was seen to have been formed, while the corresponding cell in the adjacent filament had only just put out a slight protuberance, its chloroplast also being as yet unmodified (see Fig. 1, B) ; usually, however, the two conjugating cells were in about the same stage of devlopment The two gametangia were always approximately of the same size.

At this stage the two gametangia, although organically independent, are firmly united, and rather violent treatment is required in order to separate them, although it is often done when teazing filaments apart for mounting. The binding mucilage often forms a conspicuous thick ring round the junction of the two gametangia, as mentioned and figured by de Bary, and as shown in Fig. 1, A, B. This gametangium stage seems to persist for some time, since it was rather frequently met with in conjugating filaments ; in fact the whole process of zygospore-formation in this alga takes place remarkably slowly, and must occupy some considerable time.

De Bary states that the separating-walls between the two gametes become gradually absorbed from the middle outwards, while the gametes fuse to form the zygospore. The Wyre Forest specimens, however, showed a stage, prior to fusion of the gametes, which is not mentioned by de Bary. This is the formation of a thin wall entirely surrounding each gamete (Fig. 1, C, a, and 2, A, a), and independent both of the partition-wall, which first cut off the gametangium, and of the wall of the protuberance of the conjugating-cell, although generally closely applied to both of these. This inner wall is thin and firm, is of cellulose, and easily recognised on account of its sharp contour, at any rate towards the distal end

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[1] The material was not sufficiently abundant to enable the cytology of the process to be followed by appropriate staining methods. The nucleus presumably remains in close association with the chloroplast.

of the gametangium (or apex of the protuberance), since the actual wall of the protuberance here is usually much swollen and more or less mucilaginous at this stage. At the other end of the gametangium, however, the inner membrane is not always clearly marked off from the septum which cut off the gametangium; in fact the two, being generally in such close relation to each other, often appear as a single wall, but they may be separated, and in the zygospore stage (see below) readily come apart. Thus, *prior to fusion of the gametes*, each of the latter is surrounded by a double investment, a state of affairs which appears—as far as is known at present—to be unique amongst the Conjugatæ.

In Fig. 1, C (drawn from a specimen mounted in glycerine jelly) the two gametangia have been torn apart in the mounting, and the inner wall (a) round each gamete is well shown. This might have been interpreted as being the development of twin spores (*i.e.*, two azygospores), but since all possible degrees of fusion between these double-walled gametes were observed, this view cannot be held. It is rather an expression of the great delay in the process of fusion of the gametes, for which the alga is remarkable.

Fig. 2, A, also drawn from a permanently mounted specimen, shows the commencement of fusion. The walls of the protuber- ance (c) of the conjugating cells have become much swollen and mucilaginous, and are seen to have been torn apart in the mounting. The septum (b), which cut of the gametangium in the upper cell, is retained by the cell-wall of the latter, its attachment to which is clearly shown. The upper gamete has been torn from its outer investment, but is surrounded by its inner wall (a), while the specimen shows that the latter is an independent structure The lower gametangium (in the figure) is intact and its wall obviously double.

The earliest indication of the commencement of fusion of the gametes is quite characteristic, the appearance being that shown in Fig. 1, D, a. The outer wall of each gametanginm (*i.e.*, the walls of the original protuberances) is seen to have become much swollen and mucilaginous, the line of separation between the two gametangia being lost. One of the gametes (the lower one in the figure) now puts out a conical process towards the other gamete, but the latter, instead of putting out a corresponding process, exhibits a flattening or *slight concavity* on its surface where the process impinges on it. This concavity is shown in the upper

gamete of Fig. 1, D, b, where a somewhat later stage of fusion is figured. Thus at stages a and b (Fig. 1, D) there is a distinct morphological differentiation between the gametes ; but although always to be seen in the early stages of fusion, the distinction is lost in the stage figured in Fig. 1, D, c. It seems clear, there-fore, that there is a slight sexual difference between the two gametes, the one putting out the process being looked upon as male, the other as female. The cells of any particular filament, however, do not give rise exclusively to gametes of one " sex."[1]

The ultimate product of fusion is a more or less ellipsoidal zygospore (Fig. 2, B) round which frequently an equatorial furrow often persists for some time but eventually disappears. The thin inner wall of each gametangium remains round the corresponding half of the zygote, the two membranes becoming fused together round the middle of the zygospore to form a perfectly continuous wall round the latter ; and this investment persists as the *outermost layer of the wall of the zygospore*. It is quite clear that the thin inner walls of the gametangia do not become mucilaginous like the wall of the " conjugation-canal " ; and that they persist throughout fusion of the gametes—only becoming absorbed locally in order that this can take place—and eventually join up to form the first membrane round the zygote. This membrane is undoubtedly added to as the slow fusion of the gametes proceeds, and, as the zygospore ripens, continuous layers are deposited internally, so that the wall of the mature zygospore is thick and lamellated, but remains colourless and smooth.

The mature zygospore (Fig. 2, B, C) is 26-30 μ long, 16-20 μ wide, subellipsoidal or subglobose, and resembles very closely, but is not quite so irregular as those of " *Zygnema pachydermum* " figured by W. & G. S. West (11). It is easily set free from the " conjugation-canal " since the latter becomes very mucilaginous, and sometimes almost disappears. When the zygospore is thus set free the septa, which first cut off the two gametangia, always remain behind attached to the cell-walls of their of their respective conjugating-cells (Fig. 2, A, C), and never become detached with the zygospore,

The filaments generally conjugated in an irregular fashion 3 or 4 often conjugating amongst themselves. It was always found that short lengths (of 1-10 cells) of a filament were in con-

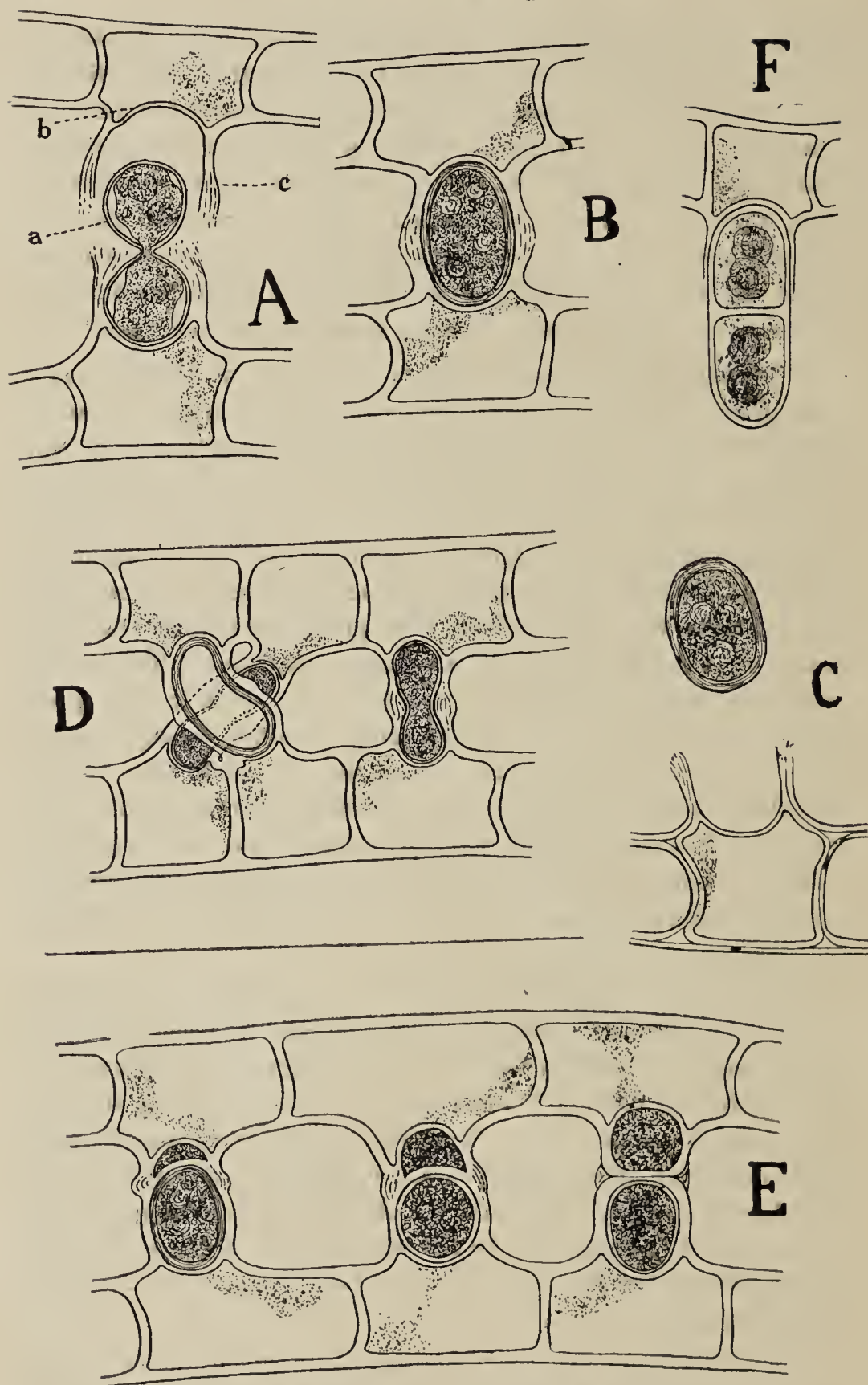[1] Cf. in this respect, " the crossed zygospores " described below.

Fig. 2, *Zygogonium cricetorum*: A, early stage in process of fusion of gametes
—for description see text; the contents of each gametangium has shrunken
somewhat owing to the mounting; B, mature zygospore; C, ditto, free from
the "conjugation-canal"; D, crossed zygospores—see text; the contents of the
topmost zygospore has been omitted in order to show the outline of the lower,
which is immature; E, three successive stages (from right to left) in the
development of an azygospore; the mature azygospore is seen on the extreme
left; F, young filament of two cells produced by the germination of a
zygospore, and attached at one end to one of the conjugating filaments.
   All × 600.

jugation with one or more other filaments, while these lengths would be separated by intervals—of variable length—of purely vegetative cells.

The four pyrenoids are sometimes recognisable in the young zygospore, and scattered starch-grains may also be present, but in the mature zygospore no pyrenoids are to be made out, and the reserve-material consists of large globules of a fatty oil, no starch being present.

The formation of *azygospores* or parthenospores was observed in a few cases, but their occurrence must have been very rare. Three successive stages (from right to left) in the development of an azygospore are shown in Fig. 2, E, from which it is clearly seen that the gametangia never fuse, but that one becomes enlarged, its contents takes on a thick lamellated cell-wall, and forms the azygospore. The latter is smaller than the zygospore (being about 22·5 μ long, and 15 μ wide), but has the same densely granular contents, and numerous oil-globules; its shape is more or less ellipsoidal. The companion gametangium degenerates, and eventually becomes a mere shrunken appendage. Although not actually observed it seems quite possible that occasionally *both* the gametangia may develop simultaneously, without fusion, to form twin zygospores.

A rather curious state of affairs is figured in Fig. 2, D, where four cells have conjugated crosswise, so that the resulting zygospores lie one above the other, and are crossed, although several other cells of the two filaments had conjugated normally. The crossed zygospores may possibly be explained by the four gametes concerned being so placed that each is directly opposite to one of its own "sex" (cf. above), while the diagonal pairs of gametes are of opposite "sexes." This, however, is only put forward as a suggestion, as the condition may be the result purely of accident.

Two examples of germinating zygospore were seen, one of which is figured (Fig. 2, F). In both cases the zygospore had elongated and divided into two exactly similar cells, while the embryo filament had retained its connection, at one end, with one of the conjugating filaments, as shown. There is no differentation into base and apex in the young filament.

III. Conclusion.

It seems clear that the above must be regarded as the normal method of conjugation of *Zygogonium ericetorum*. In what

relation then does this alga stand to "*Zygnema pachydermum*" W. & G. S. West, which, according to West and Starkey (9, 10,) is identical with *Zygog. ericetorum?* It may well be that the latter authors are correct, while the process of conjugation described for "*Z. pachydermum*" may be abnormal, and a result of the peculiar conditions under which the alga was found growing in the W. Indies. The high temperature of its habitat (a warm stream in the crater of a volcano) may have supplied the extra stimulus which induced the alga to conjugate in a more direct way, after the manner of certain species of *Zygnema.* Indeed, may not the condition found in "*Z. pachydermum*" be a reversion to the method of conjugation employed by the immediate ancestors of *Z. ericetorum?* [1] The peculiar method of conjugation, which must now be considered as normal in the latter species, was possibly derived from the ordinary *Zygnema*-method, by the fusion of the gametes being greatly delayed—a result of the lethargic and "inert" character of the alga—and a consequent need for extra protection of the gametes ; the various new stages thus being looked upon as intercalated into what was originally a method similar to that found in the species of *Zynema* in which the zygospore is lodged in the conjugation-canal.

In its cytological characters (9, 10, 4) *Zygogonium ericetorum* obviously stands in close relation to *Zygnema* and *Pyxispora*, and the three genera are best placed together as a sub-family of the family Zygnemaceæ—following the modern tendency to utilize chloroplast-characters as the basis of the subdivision of this family. It is interesting to note that, in the fact that the gametes are cut off in special gametangia, *Zygogonium ericetorum* stands in exactly the same relation to *Zygnema*, as *Sirogonium* does to *Spirogyra*, and as *Temnogametum* does to *Mougeotia.* To make the type of conjugation observed in *Zygogonium* the basis of a special sub-family in the Zygnemaceæ—as, for instance, is done by Wille (13)—seems very undesirable, as it quite obscures the obvious relationship of the genus to *Zygnema.*

The formation of the gamete from only part of the protoplast is a character which many algologists consider of great importance, Wille (13), for instance, uses it as the basis of his Mesocarpaceæ— a family which should thus logically include *Zygogonium ericetorum* and *Pyxispora*, as well as *Mougeotia* and its allies. If, however,

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[1] Nevertheless the possibility of "*Z. pachydermum*" being a species distinct from *Zygog. ericetorum*—although showing identical vegetative characters—must be borne in mind.

the principle first enunciated by Palla (6)—that chloroplast-characters rather than modes of conjugation should be used in the grouping of the various filamentous Conjugates—be accepted, then the character in question is not of more than generic importance.

There seems now no reason to doubt that *Zygogonium erice-torum*, on account of its mode of conjugation, must be placed in a genus apart from *Zygnema*. One must therefore either accept de Bary's emendation of Kützing's genus "*Zygogouium*"—as is done, for instance, by Wille (12, 13) and Borge (1), solely on the evidence brought forward by de Bary—or else create an entirely new genus for the alga. The latter course is highly undesirable, as it would only complicate matters further; and, as it has been abundantly shown (10, 8) that Kützing's genus is untenable, there seems no reason why the *Zygogouium* of de Bary should not take its place. West and Starkey (10) wrote that the " available evidence does not support the retention of *Zygogouium* on the basis put forward by de Bary (1858) and Wille (1909)." The observations given above, however, appear to supply the required evidence, so that if the genus is retained at all it must be as *Zygogonium* (Kütz.) emend. de Bary.

It may be noted, in conclusion, that the terrestrial form of *Z. ericetorum* never seems to have been recorded in conjugation before. Rabenhorst (7) states that the terrestrial forms of *Zygog. Agardh*. Rabenh. (= *Z. ericetorum*) are always sterile. Cooke (2) follows Rabenhorst, and says that some forms of *Zygog. ericetorum* are " terrestrial and always sterile, others aquatic producing zygospores." The above thus seems to be the first record of the terrestrial *Z. ericetorum* being found in conjugation. It is highly desirable that conjugating specimens of the *aquatic* form of the alga should be found and compared with what is described above It may be that the methods of conjugation of the two forms are not quite identical. For instance, the inner wall of the gametangium, described above—but not mentioned by de Bary, whose specimens were apparently of the aquatic form—may con-ceivably not be formed in the aquatic *Z. ericetorum*, in which the gametes would not be in need of such efficient means of protection against desiccation as they would be in the terrestrial form.

IV. Summary.

1. The conjugation of the terrestrial form of *Zygogonium Zygnema*) *ericetorum* has been observed, and is described.

2. De Bary's account of the conjugation of this alga (under

the name of *Zygogonium didymum* Rabenh.), as far as it goes, has been confirmed, and further details added.

3. The greater part of the protoplast of each conjugating cell passes into the protuberance put out by the latter, and is there cut off as a special gametangium by a curved partition wall. Later, each gamete secretes a thin, independent cell-wall entirely round itself. Thus, prior to fusion, each of the gametes is surrounded by a double investment.

4. In the early stages of fusion of the gametes, the latter show a slight morphological distinction.

5. The inner walls of the two gametangia become only locally absorbed during fusion of the gametes, and unite to form a continuous membrane round the zygote; and this membrane persists as the outermost layer of the wall of the zygospore.

6. The development of azygospores was observed, and is described.

7. The relation of *Zygogonium ericetorum* to " *Zygnema pachydermum* " W. & G. S. West is discussed.

8. The writer supports the retention of the genus *Zygogonium* on the basis proposed by de Bary (1858), and accepted by Wille (1897, 1909), and others.

I wish to express my thanks to Professor G. S. West, to whom I submitted specimens of the alga, for helpful criticism and advice on several points in connection with the paper.

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THE RECONSTRUCTION OF ELEMENTARY BOTANICAL TEACHING.

BOTANY AS THE SCIENCE OF THE LIVING PLANT.

To the Editor of The New Phytologist.

Dear Sir,

As one who is deeply convinced of the important part Botany and its applications have to play in the national life of the future, I am glad to take the opportunity afforded by the discussion in your pages on the Reconstruction of Elementary Botanical Teaching to state my opinions on the matter.

With much of the original memorandum I am in complete agreement. It is obvious that the importance of botany in comparison with other sciences is not generally realised, and it is clear that this must be due to botanists themselves and their presentation of their subject, at any rate in part. I also agree with the signatories of the memorandum that the disgracefully small remuneration offered to botanists, the paucity of adequately paid research posts, and one may add, the almost universal understaffing of botanical departments, all play their part, and in my opinion, a very large part, in producing the present situation. The events of the past twenty-five years suggest that the only effective way of bringing about improvement in these particular matters is by collective action on the part of botanical workers. The recent formation of the National Union of Scientific Workers has now made this possible, and it seems to me the duty of every botanist who wishes to improve his subject to join the Union.

But as the memorandum deals especially with teaching, I

will not enlarge on the position and status of the professional botanist, but pass on at once to the question of reconstruction of teaching. There can be no doubt that in many departments improvement can be effected. But we must realise at the outset that in arranging courses what we have to aim at is to give a properly balanced presentation of the subject in relation to the ultimate object of our students in attending the course. An elementary course of botany to medical students obviously can with advantage differ from an elementary course of botany to students who intend to become professional botanists. In many botanical departments the same elementary course is provided for all students taking the subject, whatever their reason for so doing. It seems clear that in such cases the first stage in reconstruction should be to separate students into different classes according to their purpose in taking the subject. In Leeds we arranged special courses for students taking Medical, Science and Arts degrees as long ago as 1912. But to give three courses instead of one naturally means three times as much work, and obviously the enlargement of the teaching staff may be necessary to bring about this first stage in improvement.

Again local conditions must always play a part in determining the content and arrangement of courses.

But on the whole the contention of the signatories of the memorandum that the teaching of botany in this country has a morphological bias which works to the detriment of physiology and those aspects of botany with an outlook on practical life is no doubt true. Nevertheless the problem does not strike me as one of morphology against physiology. As the signatories of the memorandum say, it is not the introduction of more physiology in place of some of the morphology that is wanted, it is not patching but reconstruction, a complete change of outlook, that is desirable.

Well, I stand for the doctrine of Botany as the Science of the Living Plant. I can make no claim to originality in this conception, for it was the motive underlying the work of A. T. Knight nearly a century ago. Recently Professor Ganong has written a book with the title of "The Living Plant." Less than two years ago Professor Hans Fitting delivered an academical oration with the title "Die Pflanze als lebender Organismus." In the correspondence in these columns Professor Bower claims that he teaches the Living Plant. Dr. Keeble, one of the signatories of the memorandum, has, as I interpret it, recently expressed the same

idea when he said "Cultivate the laboratory a little less, and our gardens rather more" (*Science and the Nation*, p. 128). Personally I should have preferred "Cultivate the laboratory a little more and the garden a lot more." These references will make it clear that the idea of botany as the science of the Living Plant is one that has borne itself in on the minds of botanists in different parts of the world.

It seems to me then that among other things that are wanted to revivify botany, to bring it into the position it ought to occupy, is to think of it and teach it as the science of the Living Plant. In its earlier stages a systematic study of external form, botany developed during the latter half of the nineteenth century into a systematic study of internal structures having for its ultimate aim the construction of the genealogical tree of the plant kingdom. Along with this morphological study, but occupying in this country a decidedly subsidiary position, proceeded the investigation of the mechanism of the plant. This aspect of botany, plant physiology, has tended to become more and more a biochemical and biophysical study of isolated plant organs and isolated plant processes. This biochemical physiology is almost as far removed in its way from the Science of the Living Plant as morphology subordinated to phylogeny. Neither has more than a passing interest in the living organism as such.

It is clear that if the present tendencies are persisted in they must inevitably lead to the divorce of morphological from physiological botany. This I feel would be disastrous. I do most emphatically belong to that school of thought which holds that the splitting up of the science into separate water-tight compartments would be bad for all branches of the subject. The evils attendant on the splitting up of the subject have been dealt with in the original memorandum. I agree entirely with the remarks on the matter made therein, and I need not deal further with this question.

But if botany is treated with the Living Plant as its central theme it will embrace morphology and physiology, as well as those more recent and from an economic view, most important developments, such as genetics and plant breeding, plant pathology, ecology, which would not be included either in morphology or physiology in the commonly accepted narrow sense of these terms. These younger studies are most decidedly and essentially aspects of the Science of the Living Plant, and when one considers how ill many

elementary courses provide for them, one realises how far we are from thinking of Botany as the Science of the Living Plant.

But it is not so much a change in the content of elementary courses that seems to be desirable, as a modification of the mode of presentation of the material, so that instead of giving the impression of the all-importance of the construction of evolutionary trees or the expression of the activities of particular organs in terms of biochemistry, we should teach it as a science of living organisms, in which the central theme should be the mode of living of the plant, how it undergoes development both in its ontogeny and phylogeny, how it maintains its life processes and how these are intimately related with the structure of the organism and the environment, how plants vary in their form and mode of living and how they solve the problems of existence in different ways, their relations one to another, and so on.

This is not in any sense a syllabus of a course ; it is simply a crude statement of the fundamental fact that botany differs from chemistry or geology chiefly in the fact that it is the study of living matter and not of non-living material.

Without going further into detail I may refer at once to two elementary text-books of botany which appear to me to present the subject of Botany from the desired point of view. One is Timiriazeff's " Life of the Plant," the other is Gager's " Fundamentals of Botany." The former will undoubtedly be considered too physiological by most botanists for a model of an elementary course of botany, but the same criticism cannot be levelled against Gager's book. This work in my opinion indicates as nearly as possible the scope of an elementary course of botany from the standpoint of the Living Plant, such as would be desirable to give at the present time. I think any morphologist will readily admit that his special interests are not side-tracked, for about three quarters of the book deals with the structures and life histories of various forms throughout the plant kingdom, and the selection of types is perfectly orthodox. But the general presentation of the subject matter is such that one always realises that it is a living organism with which one is dealing, and not merely a body of a certain form and struture, nor yet simply a complex chemical system which undergoes certain reactions.

A course such as that presented in Gager's " Fundamentals of Botany " seems to me then a suitable introduction to Botany as the Science of the Living Plant. A nearer definition of a course

would be purposeless, as local conditions and personal inclinations of the teacher will, let us hope, always be responsible for wide differences in the teaching programme in different places. There is nothing ideal in a monotonous uniformity.

The introductory course, by which I mean that provided for students preparing for Intermediate B.Sc. examinations or those of a similar standard, would be succeeded by intermediate courses in which the student would have an opportunity of a more intimate acquaintance with the methods of morphology and phylogeny, physiology, genetics and pathology. I think this can be done without the expenditure of more time than is already devoted to a Pass B. Sc. course, nor does it involve generally speaking any great change of subject matter, though in many institutions no doubt a certain amount of morphology could be sacrificed at this stage without harm resulting. But it does seem to me that a student in his Final B. Sc. course should be given a working acquaintance with those aspects of botany which are of economic importance. We must always keep in view the aims of students and remember that the majority have to earn a living. I fully agree with the original memorandum that we should provide teaching with an outlook on practical life. One of your correspondents objects to this view apparently on the ground that because a distinguished botanist was fortunate enough to be able to choose her own line of work without hindrance, therefore "the great inheritance of the Universities is the tradition of learning for learning's sake." This all seems beside the mark. We do not deprecate learning for learning's sake because we hold that University courses should consider the objects and economic interests of those who attend them. I am interested in mediaeval church architecture and in natural scenery, but I should never suggest that courses in architecture and geology should be arranged to suit amateurs like me who are interested in them for their own sake, rather than for those who have to design buildings or survey for minerals in order to get their daily bread. The same is true in regard to botany; we must see to it that those aspects of botany which are of economic importance find a place in our courses.

The study of ecology is a difficulty. Ecology is, or should be entirely a study of the Living Plant, but I agree with Dr. Jeffreys as to the difficulty of its presentation in an elementary course. But undoubtedly field work should occupy a much greater

proportion of our teaching than it does at present in most Universities, and the field excursion should be the actual, as well as the logical, means of introducing students to plants in relation to their natural environment.

Finally in the spirit of Dr. Keeble's remark cited earlier, one may conclude with Voltaire, and literally : " Il faut cultiver notre jardin."

There are a few words I should like to add in regard to examinations. These I have always felt constitute an evil which is tolerated because there appears to be no better way of testing an elementary student's grasp of a subject. But we want as few examinations as possible. Thus I fail to see why, as one of your correspondents would have it, " it is essential that a student should not be allowed to take an Honours degree in any subject without first taking the Pass." This suggestion, if carried into effect, would as far as I can see, benefit no one but the professional examiner who is paid according to the number of candidates he examines. Surely any teacher can judge whether a student is undoubtedly fit to take an honours examination or not. A candidate for honours should only be forced to take a pass degree if his ability to pass an honours examination is a matter of doubt to his teacher.

I should also add that any remarks I have made in regard to the position of pure morphology and biochemical physiology in the teaching of elementary botany are not to be interpreted as applying to research. Research work in pure morphology and in the physiology of organs is as essential as research in any other branch of botany, both from the point of view of the acquisition of pure knowledge and the obtaining of information of economic importance. But a consideration of research is outside the scope of this discussion.

To sum up, an improvement in the position occupied by botany among the sciences is to be attained (1) by collective action of botanists in order to bring about improved conditions and status for the professional botanist, (2) by a re-orientation of the point of view from which elementary botany is taught so that emphasis is laid on Botany as the Science of the Living Plant rather than as a study of phylogeny or a biochemical study of plant organs or plant processes. Such a changed point of view would necessarily involve the laying of increased emphasis on those aspects of botany which are of economic importance.

As far as I am aware such a change of view can be introduced to-morrow into the courses in the botanical departments of any University in Britain if the head of the department so wishes it, with the exception perhaps of the Universities of London and Wales. In the case of the former surely the signatories of the memorandum have enough influence to effect the changes they desire. We who are younger and uninfluential look to them to show us the way.

I remain, dear Sir,

Yours faithfully,

WALTER STILES.

BOTANY DEPARTMENT,   INSTITUTE OF PHYSIOLOGY,
                      AND
    THE UNIVERSITY, LEEDS   UNIVERSITY COLLEGE. LONDON.

16th November 1918.

A VOICE FROM THE SECONDARY SCHOOLS.

To the Editor of THE NEW PHYTOLOGIST.

SIR,

It has been suggested to me that a contribution to this discussion from the point of view of the secondary school teacher may be of some interest, and I should like to call attention to one aspect of the question which has scarcely been mentioned by previous contributors, namely the importance of the method of teaching as well as of what is taught. While we are coming more and more to consider the plant as a living active organism, let us not forget to regard the minds of our pupils in the same light, rather than as passive receptacles for receiving knowledge. It seems to me that one of the chief values of botany as a subject of education is the possibility it affords for training in original observation, accuracy, and reasoning; but its usefulness in these respects is largely determined by the manner in which it is taught, especially in elementary classes. For example, what training in observation is afforded by morphology when the method is first to give a descriptive lecture on a plant or group of plants, and afterwards to supply the students with material showing the facts mentioned? Or what practice in reasoning by physiology when it is first stated for a fact that certain processes take place in plants, and then the students are invited to perform or witness certain routine experiments to verify the statements made? Surely not only must the study of function be more closely associated with that of structure, but there should also be a far closer union of theory and practical work than we have been accustomed to in the past. I

feel strongly that in elementary classes the theory should be allowed to arise mainly from the observational and experimental work of the students themselves, the teacher's function being to guide the practical work and discussion and call attention to related facts and phenomena as need arises, the centre of gravity of the teaching thus being shifted from the lecture room to the laboratory. The treatment of physiology, for example, as a series of problems which the class is to suggest means of investigating, and then to carry out the experiments suggested after discussion of the best means of doing them, without being told the results and conclusions beforehand, should do much towards giving the new spirit in elementary work which most of your contributors agree is necessary and also lead to a better understanding of the significance of scientific method. True, there are difficulties in the way—lack of time, rigid examination syllabuses, large size of classes, dependence on progress in related subjects such as chemistry, and the necessity of dovetailing different sections of the work according to the seasons (the scheme of "one term one subject" looks particularly awkward from this point of view)—but I am convinced that it would be well worth while, especially for prospective teachers, if even only a part of the elementary course, say the first year, could be reorganised on such lines.

With regard to the various suggestions made during this discussion, I am entirely in favour of teaching function and conditions of life as far as possible in connection with morphology and structure, and the developing of points of contact with various branches of practical life (with schoolgirls, applications of botanical facts to cookery occasionally prove of interest), though I agree with "Witness" and others as to the impracticability of introducing a large amount of ecology into the elementary course. I should like to support the suggestion that "The Five Wise Men" be invited to publish a specimen syllabus of work, and also the proposal that examination schedules should not be rigidly detailed.

The proposal to include practical garden work in the University botany course would be particularly useful to intending teachers, in view of the growing movement in favour of school gardening, provided that the connection between theory and practice were clearly insisted on, and the instruction given such as would fit the student to plan and work a garden unaided, but the large amount of time required is one great difficulty of organising gardening in connection with the teaching of botany.

Yours etc.

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Merthyr Tydfil.

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